DIVISION OF BIOLOGICAL RESEARCH
COLLECTED REPRINTS
1962

VOLUME I

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BUREAU OF COMMERCIAL FISHERIES

FISH AND WILDLIFE SERVICE

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Review: *Fauna e Flora del Golfo di Napoli. Monografia 38: Uova, Larve e Stadi Giovanili di Teleostei*

Elbert H. Ahlstrom

FAUNA E FLORA DEL GOLFO DI NAPOLI. MONOGRAFIA 38: UOVA LARVE E STADI GIOVANILI DI TELE OSTEI. Monografi elaborata con l'uso de materiale raccolto e seriato da Salvatore Lo Bianco. Authors include Umberto D'An cona, Luigi Sanzo, Antonio Sparta, Fausta Bertolini, Giuseppe Montalenti, Emanuele Padoa, Silvio Ranzi, Enrico Tortonese, and Maffo Vialli. Pubblicata dalla Stazione Zo ologica di Napoli. Published in four parts between 1931 and 1956. 1,064 pages, 831 text figs., 51 plates.

The monograph of the eggs, larvae, and juveniles of teleost fishes in the vicinity of Naples is the most comprehensive work of its kind on the younger stages of fishes. The work was initiated and published by the Zoological Station of Naples. It was issued over a 25-year period, part 1 appearing on 15 December 1931, part 2 on 21 (25) April 1933, part 3A in 1937, part 3B on 31 October 1956.

I was requested to prepare this review because the monograph had not been reviewed in *Copeia* previously, and is not as widely known as it deserves to be. Considering the size of the work and the excellent illustrations, many in color, the price I paid for my set, approximately $81, is not exorbitant.

There is no credit given in the publication to the general editor (or editors) of the monograph who coordinated the work of nine scientists and seven artists, and

drew together the comprehensive bibliography and index. Umberto D'Ancona prepared the preface. There is no doubt about the inspiring force that motivated the work, however: it was Salvatore Lo Bianco. This scientist had published a series of papers dealing with the younger stages of fishes between 1888 and 1913; more important he had begun a project of collecting and illustrating the developmental stages of Mediterranean fishes, using the artistic talents of C. Merculiano and V. Serino. The project was commenced at least by 1898, hence some 58 years separated the initiation and completion of this work. Lo Bianco, in turn, had been influenced by the work of C. Emery and F. Raffaele, who had worked on developmental stages of fishes at the Zoological Station of Naples between 1878 and 1898. Raffaele had worked up developmental series for some 30 fishes.

Three aspects of the monograph will be commented upon in turn: the original figures contained in 51 plates, the text figures, and the text.

The original illustrations in the work are an artistic joy. Many are in color. The plates are large, 8″ × 11″ in overall dimensions. At the bottom of each plate are listed the scientist (or scientists) directing the work and the artist drawing each illustration. On a facing page is a key to the illustrations, giving the species illustrated, and for each figure the size of the specimen and its magnification in the drawing. The two principal artists are V. Serino and C. Merculiano; F. Mazza has illustrated the sections edited by L. Sanzo and A. Sparta; M. Ovcinnicova has supplied illustrations for D'Ancona's section on Synentognathi; while M. Federico and P. Antonuccio have supplied moderate numbers of drawings. In all, 157 species are illustrated in the 800 original drawings that make up the plates.

An even more comprehensive group of illustrations are included in the text. These are numbered through 831. There is no consistency in numbering; each specimen of egg or larva is given a separate text figure number in most instances, but in some sections of the monograph as many as six or seven illustrations are included under one text figure number. Most text figures are copies of published illustrations, a few are original drawings. They vary in quality with source, but bring together a larger body of embryonic and larval fish illustrations than is contained in any other work, including Ehrenbaum's (1905–1909), "Eier und Larven von Fischen des Nordischen Planktons." The work of L. Sanzo has been drawn upon for more text illustrations than that of any other investigator. Raffaele is well represented, as is Ehrenbaum and Fage. Classic studies in the development of particular groups, such as those of Schmidt on gadids, Grassi on eels, Tåning on myctophids, Kyle on bothid flatfish, and Peterson on gobies are the main sources of text figures for these respective groups. The text figures chosen range from excellent to fair, but their quality, on the whole, is high. Many are reproduced somewhat larger than are the original illustrations in the plates, which is an advantage.

The text is the work of nine scientists, some of whom are widely known specialists in fish development, i.e., L. Sanzo, A. Sparta, and U. D'Ancona; others are unknown to me except for their contributions to the monograph. U. D'Ancona and E. Padoa have made the largest individual contributions, each preparing ten sections. L. Sanzo has prepared the sections dealing with salmonids, stomiatids, macrurids, and zeomorphs; Sparta's principal contribution is the development of scorpaenids. S. Ranzi has contributed the section on his specialty, the sparids; this is the best illustrated section in the monograph utilizing nine complete plates. F. Bertolini has written the sections on apogonids and serranids; G. Montalenti on maenids, mullids, sciaenids, and cepolids; and M. Vialli on atherinids, mugilids, and sphyraenids. E. Tortonese has given a revised check list of Mediterranean fishes (pp. 979–989) in addition to editing the sections on Iniomi and Pediculati.

The text, of course, is in Italian. Fortunately, Italian is one of the less difficult languages to translate. A person acquainted with any of the Romance languages and in possession of a good Italian dictionary can soon make sense of the text. His reward may not be commensurate with the effort expended, however. Many words are wasted on the static approach to larval description, which usually tells in a paragraph about each of several sizes of larvae what one can see in a glance at the accompanying figures. The text isn't bad of its kind; it is just

that I have little patience with the naturalistic approach to larval development. The dynamic approach to the study of fish development is so much more thorough, more informative, more basic.

The Italians have given us the best regional monograph available on the eggs, larvae, and juveniles of teleost fishes. In a real sense it is a work of art: it shows what the scientific artist can achieve. It is not a complete fulfillment of what the scientist should achieve, however. It will aid the biologists taking the next, necessary step, and is an indispensable reference volume for all workers in teleost development.

Don't rush to the Stazione Zoologica di Napoli to study egg and larval development. Their interest in this field is now historical, as I learned during a visit in 1959.—Elbert H. Ahlstrom, *U. S. Bureau of Commercial Fisheries, Biological Laboratory, La Jolla, California.*

Methodological Paper No. 5

FLUCTUATIONS AND FISHING

by

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Abstract

Fluctuations in the catch of a pelagic fish population arise primarily from flucutations in (a) population size, (b) availability (accessibility), and (c) fishing effort.

It is difficult to obtain adequate measure either of population size or of the unavailable portion of a pelagic fish population, such as that of the Pacific sardine. Estimates of population size based on catch, effort and age data are unreliable due to varying availability. Independent or semi-independent estimates of population size and distribution of the Pacific sardine are being obtained from (a) spawning surveys, and (b) fish scouting surveys that cover the distributional range of the fishery stocks.

Fluctuations in population size arise primarily from fluctuations in the success of year broods. Environmental factors appear to play the dominating role in determining the success or failure of year classes. The effect of fishing on recruitment would be an indirect one, resulting from reduction of spawning stock. There has been no demonstrable relation between the number of eggs spawned by a pelagic marine fish and the size of a year class. If there is a relation between spawning stock size and the size of the resulting year class, it is masked by the more dominating environmental effects.

LES FLUCTUATIONS ET LA PECHE

Résumé

Les fluctuations de la pêche des poissons pélagiques sont dues principalement aux variations : a) de l'importance de la population; b) de la disponibilité (accessibilité) et c) de l'effort de pêche.

Il est difficile de déterminer avec précision l'importance d'une population ou la partie non disponible d'une population pélagique telle que la sardine du Pacifique. Les estimations de population fondées sur les quantités pêchées, l'effort de pêche et l'âge des individus ne sont pas valables en raison des variations de la disponibilité. Des estimations indépendantes ou semi-indépendantes de l'importance et de la distribution de la sardine du Pacifique sont obtenues par a) des enquêtes sur le frai et b) des enquêtes d'exploration du poisson couvrant l'aire de distribution des populations pêchées.

Les variations de l'importance de la population sont dues principalement aux fluctuations des résultats de l'alevinage. Les facteurs écologiques semblent jouer un rôle déterminant dans la réussite de la catégorie des individus d'un an. La pêche n'aurait qu'un effet indirect, en réduisant le nombre d'individus susceptibles de frayer. On n'a pas pu établir un rapport valable entre le nombre d'oeufs pondus par un poisson pélagique et le nombre d'individus d'une classe. S'il existe une relation entre le nombre d'individus qui fraient et celui de la catégorie d'âge qui en résulte, elle est masquée par l'influence plus marquée du milieu.

FLUCTUACIONES Y PESCA

Extract

Las alternativas de la captura de especies pelágicas obedecen principalmente a las fluctuaciones (a) del volumen de su población, (b) de la accesibilidad y (c) del esfuerzo pesquero.

Es difícil obtener una adecuada medida del volumen o de la parte inaccesible de una población pelágica como la de la sardina del Pacífico. Como la accesibilidad es variable, las estimaciones del volumen de población a base de la captura, del esfuerzo pesquero y de los datos sobre la edad son enseguras. Para obtener estimaciones independientes o semi-independientes del volumen de población y de la distribución de la sardina del Pacífico se recurre (a) a investigaciones sobre el desove y (b) a exploraciones o reconocimientos de la zona de dispersión de la especie.

Las fluctuaciones del volumen de población se deben primordialmente a variaciones en los resultados de la cría anual. Los factores ecológicos parecen desempenar una función predominante en la determinación del éxito o fracaso de las clases anuales. Los efectos de la pesca se reflejarán indirectamente en el reclutamiento como consecuencia de la reducción del número de hembras en desove. No se ha podido demostrar la existencia de una relación entre el número de huevos depositados por una especia pelágica marina y el volumen de una clase anual. Si entre el número de hembras en desove y el volumen de la clase anual subsiguiente existe alguna relación, los efectos ecológicos más predominantes la ocultan.

1 FLUCTUATIONS AND FISHING

Fishery biologists are very aware of the marked fluctuations that occur in the catches of marine fishes. Workers investigating sardines are especially aware of such fluctuations.

1.1 Causes of fluctuations in catch

Fluctuations in the catch of a fish population can arise primarily from one of the three causes :

(a) Fluctuations in population size;
(b) Fluctuations in the degree of availability of the population to the fishery;
(c) Fluctuations in fishing effort.

The only way that man can affect the population of a pelagic marine schooling fish such as the sardine, is by fishing. Another set of problems involves man's effect on anadromous fishes, by pollution of rivers, construction of dams, etc., but these need not concern us. Neither shall we consider such limited aids in replenishing stocks as hatchery reared fish or transplants, even though the latter has been shown to be of some importance in management of demersal species (especially plaice; Tåning, 1952).

1.2 Management of a fishery

The theory behind management of a fishery is that favourable changes can be derived by controlling the amount of fishing or the method of fishing.

There are only two important ways in which management can affect the catch : (a) by regulating the catch of the recruited population to obtain the most favourable yield per recruit, and (b) by regulating the catch of potential spawners to ensure a spawning stock of sufficient size to maintain a high level of recruitment. The objective of such regulation is to obtain what is variously referred to as the maximum sustained yield, the maximum equilibrium catch, or the optimum catch.

1.2.1 Yield-per-recruit

The yield-per-recruit is dependent upon four interacting factors : (a) the portion of the population taken annually by fishing effort (fishing mortality), (b) the portion of the population that dies annually from causes other than fishing (natural mortality), (c) the growth pattern, and (d) age at first capture. For any fishery for which these factors are known, it is possible to derive estimates of the yield-per-recruit that can be obtained under different combinations of mortalities and ages at first capture. If growth is density dependent, this adds a complicating feature to the determinations. The author is not considering the effect of economic factors on yield-per-recruit. There is general (although not universal) agreement among fishery biologists that favourable changes in the quantity and quality of fish landed can be obtained for some fisheries by basing regulation on yield-per-recruit data.

The favourable effects that have been obtained in some demersal fisheries by regulating the mesh size of trawls are too well documented to need more than a passing notice.

In some fisheries there are considerations which preclude obtaining the greatest yield-per-recruit, at least in weight. As Huntsman (1953) noted : "The highest take is not necessarily the best." If yearlings are preferred for canning, as in the case of the American herring industry, quality must be given preference over considerations of quantity.

1.2.2 Spawning population

The effectiveness of management by regulating the catch of potential spawners to ensure a high level of recruitment depends upon a relation between spawning stock size and the size of the resulting year class.

As Sette (1943) pointed out, the survival of a year class is affected by extrinsic and intrinsic influences. Extrinsic influences are independent of the size of the population, and include hydrographic conditions that may influence the amount of spawning and the survival of the young, and such biotic factors as competition with and predation by other marine animals, and fluctuations in the quantity and quality of food. Intrinsic influences include the direct influence of population numbers on the amount of spawn produced and the competitive effects of population numbers on growth and survival of young.

Schaefer (1954) postulated that intrinsic influences would depend upon the state of the population with regard to its natural rate of increase according to the Verhulst-Pearl logistic. The population is assumed to have its greatest rate of increase at a middling size, and a lessening rate of increase in either direction from this size. The population is assumed to be increasing at its maximum when the abundance reaches a value corresponding to the inflection of the sigmoid growth curve [1/]

Man can only control the intrinsic influences by regulating the amount of effort in a fishery. The favourable effects of regulation will depend upon the relative importance of intrinsic influences in controlling year class size and growth as opposed to extrinsic influences. This problem will be discussed in a later section.

2 THE PACIFIC SARDINE FISHERY

Preparatory to writing this paper, the author reviewed a number of works dealing with fish population dynamics, and was impressed anew with the rapidity of the growth of this field, which lead to the comprehensive volume of Beverton and Holt (1957). Much of the theory has been built up around two species - plaice and haddock - and hence, much is not applicable to the sardine fishery. Instead of trying to deal with sardines, even in general, the writer will restrict himself mostly to a consideration of the Pacific sardine. As background, a brief description will be given of the Pacific sardine fishery and the research programmes.

1/ For an evaluation of this approach, refer to Beverton and Holt (1957)

The Pacific sardine occurs from southeast Alaska to Cape San Lucas, Baja California, and in the Gulf of California. The fishery for sardines received its initial impetus during the First World War, before which it was a minor fishery. Between the 1916-17 and 1936-37 seasons, landings increased from 27,000 to 791,000 tons. The 1936-37 season was the peak season of the fishery. During the following decade (nine seasons, to be exact), the catch fluctuated around a level of 550,000 tons. Beginning with the 1946-47 season, the catch began a decline which reached a low point in the 1953-54 season of 10,000 tons. The catch during the past season, 1958-59, was 110,000 tons.

Fishing effort has never been distributed over the complete range of the species. Most sardines caught in California have been landed at three ports : San Pedro, Monterey and San Francisco. The radius of the fishery around each port is less than 100 miles, and most catches are made within a 50-mile radius. The fishery in the Pacific Northwest has centred around the Vancouver Island area of British Columbia, Gray's Harbor area of Washington, and the vicinity of the Columbia River with landings at Astoria, Oregon. In recent years a fishery, as yet small, has developed in Baja California, with most landings at Ensenada. The landings in the several fishing areas are given in Table I. Landings at San Diego are included for completeness.

The decline in the fishery began in the Pacific Northwest and progressed southward. The last California port to be affected was San Pedro, where the 1950-51 catch was the largest in its history. Since the 1952-53 season, the catch has been variable, small, and highly influenced by availability.

Catches are made with round haul nets. During the past three decades, most catches have been made with purse seine nets, but during the first decade of the fishery the lampara net was the common gear.

2.1 Fishery investigations on the Pacific sardine

The sardine fishery is one of the more intensively investigated fisheries. Research, still in progress, was inaugurated by the California Department of Fish and Game in 1919, under the direction of W.F. Thompson. The Bureau of Commercial Fisheries set up a research group in 1937, under the direction of O.E. Sette. The Research during the past decade has been carried out on a greatly augmented scale by the California Cooperative Oceanic Fisheries Investigations (CCOFI), and the two older agencies have been joined by the Scripps Institution of Oceanography, the California Academy of Sciences, and the Hopkins Marine Station of Stanford University.

Two papers dealing with the Pacific sardine are worthy of special notice, i.e. Sette (1943), and Clark and Marr (1955). Much of the information included here has been more thoroughly documented in these papers.

Table I

CATCH OF PACIFIC SARDINE IN THOUSANDS OF TONS, 1916-17 THROUGH 1958-59

Season	British Columbia	Washington	Oregon	Floating plants	San Francisco	Monterey	San Pedro	San Diego	Ensenada	Total
1916-17	-	-	-	-	-	8	17	2	-	27
1917-18	<1	-	-	-	<1	24	41	7	-	72
1918-19	4	-	-	-	<1	36	33	7	-	80
1919-20	3	-	-	-	1	43	17	6	-	70
1920-21	4	-	-	-	<1	25	12	2	-	43
1921-22	1	-	-	-	<1	16	19	1	-	37
1922-23	1	-	-	-	<1	29	33	3	-	66
1923-24	1	-	-	-	<1	46	35	3	-	85
1924-25	1	-	-	-	1	67	96	9	-	174
1925-26	16	-	-	-	1	69	62	6	-	154
1926-27	48	-	-	-	4	82	65	2	-	201
1927-28	68	-	-	-	17	98	68	5	-	256
1928-29	81	-	-	-	14	120	119	1	-	335
1929-30	86	-	-	-	22	160	141	3	-	412
1930-31	75	-	-	11	26	110	38	<1	-	260
1931-32	74	-	-	31	22	69	43	<1	-	239
1932-33	44	-	-	59	19	90	84	<1	-	296
1933-34	4	-	-	68	36	152	125	2	-	387
1934-35	43	-	-	116	69	231	179	5	-	643
1935-36	45	<1	26	151	76	184	138	11	-	631
1936-37	44	7	14	236	141	207	138	5	-	792
1937-38	48	17	17	68	134	105	110	<1	-	499
1938-39	52	26	17	44	201	181	146	3	-	670
1939-40	6	18	22	-	212	228	102	<1	-	588
1940-41	29	1	3	-	118	166	176	1	-	494
1941-42	60	17	16	-	187	250	149	2	-	681
1942-43	66	1	2	-	116	184	202	3	-	574
1943-44	89	10	2	-	127	214	135	3	-	580
1944-45	59	<1	-	-	137	237	178	3	-	614
1945-46	34	2	<1	-	84	146	173	1	-	440
1946-47	3	6	4	-	3	25	196	5	-	242
1947-48	<1	1	7	-	<1	12	96	2	-	118
1948-49	-	-	6	-	1	35	121	3	-	166
1949-50	-	-	-	-	18	128	185	3	-	334
1950-51	-	-	-	-	13	32	303	3	-	351
1951-52	-	-	-	-	-	16	110	1	9	136
1952-53	-	-	-	-	-	<1	4	<1	7	11
1953-54	-	-	-	-	-	-	3	<1	7	10
1954-55	-	-	-	-	-	1	66	1	9	77
1955-56	-	-	-	-	-	-	73	-	2	75
1956-57	-	-	-	-	-	<1	33	-	6	39
1957-58	-	-	-	-	-	-	21	-	3	24
1958-59	-	-	-	-	-	25	78	-	8	111

The sources of some of the pertinent data concerning the Pacific sardine fishery are briefly summarized in the following sections.

- Catch, effort and age data

Length frequency data of landings are available from 1919. Much of this has been summarized by Calderwood (1953). Age composition of the landings has been determined routinely since the 1941-42 season (Felin and Phillips, 1948, and yearly supplements). Mosher and Eckles (1954) extended the age data back to the 1932-33 through 1937-38 seasons for some ports. Catch-per-unit-of-effort data for Californian ports extends back to the 1932-33 seasons (Clark, 1939; Silliman and Clark, 1945; Clark and Daugherty, 1950 and 1952; Clark, 1956). Thus catch, effort and age data for the California fishery are available for nearly a quarter of a century. Effort measures for the British Columbia fishery during 1925-32 were derived by Hart (1933); for the Oregon and Washington fisheries during 1935-43 by Marr (1950).

- Tagging data

Tagging experiments, conducted between 1935 and 1942 (Clark and Jannsen, 1945) demonstrated extensive movements and mixing of fish from the several fishing areas. Estimates of mortality rates and population size have been variously interpreted from the tagging data (Clark and Marr, 1955, especially pp. 19-20, 27-28).

- Population heterogeneity

Despite the extensive movements of fish demonstrated from tagging, there is considerable evidence that the mixing is incomplete. Phillips (1948) called attention to the differences in growth patterns of sardines from the major fishing areas, especially the difference in average size of fish of the same age landed at San Pedro and British Columbia. Felin (1954) used growth and vital statistics to support the thesis that there was considerable population heterogeneity in the Pacific sardine.

3 ESTIMATES OF POPULATION SIZE

Fluctuations in the catch of a fish population arise primarily from flucutations in population size, availability, and fishing effort. Before considering "fluctuations" in these three parameters, it is essential to consider how well we can measure each.

There is no simple way to obtain an adequate estimate of population size of a pelagic marine schooling fish. The usual data available are catch, effort, age and growth. These data would be fairly adequate if reliable information were also obtained on availability and natural mortality, but these latter data are usually lacking. Hence, it is desirable to obtain estimates of population size from as many independent methods as possible.

Among the methods for obtaining independent or semi-independent estimates of population size are tagging, surveys of amount of spawning, and surveys that assess the relative

proportions of the population in fished and non-fished areas.

3.1 Estimates of population size based on catch, effort and age data

Many papers have been written on the use of catch, effort and age data in estimating population size. In a fishery such as the Pacific sardine, the two parameters that cannot be effectively estimated from the fishery data are availability and natural mortality. Silliman (1943) developed a method for separating natural mortality from fishing mortality, by assuming that effort was the variable parameter, while natural mortality, recruitment, and availability were constant during two "stabilized" levels of exploitation of the Pacific sardine. Widrig (1954) elaborated the above method, and then considered the effects of changing availability (Section 4.1.3) and natural mortality rates on population estimates. These and additional methods of separating natural from fishing mortality are discussed by Beverton and Holt (1956). Yamanaka (1956) appraised the difficulties in estimating natural mortalities.

Estimates of population size of the Pacific sardine based on fishery data are summarized in Clark and Marr (1955). Because of the difficulties in assessing natural mortality rates and availability, several estimates based on different premises are given for each season.

3.2 Virtual population on estimates (accumulated age estimates)

In a fishery where age data are available, one of the simplest estimates of population size to derive is that of the virtual population. This is a minimal estimate of the population present during a given season, based on the catch of that season and the catches of the same year classes in succeeding seasons. The estimate is minimal because it does not take into account fish which were present in the fishing area but died naturally, or fish which were unavailable to the fishery and eventually died naturally. Developed independently for sardine population estimates under the term "accumulated age estimates" (first published in Clark and Marr, 1955), the estimate is equivalent to the virtual population estimate of Fry (1949) (see Ricker, 1958).

3.3 Estimates derived from tagging data

The tag and recapture method can be used to obtain estimates of fishing and total mortalitie and of population size. The internal metal tag, first developed by Rounsefell and Dahlgren (1933) has been widely used in studies on pelagic schooling fish : Pacific herring (Rounsefell and Dahlgren, 1933), Pacific sardine (Clark and Jannsen, 1945), Pacific mackerel (Fry and Roedel, 1949), and, more recently, Atlantic herring (Fridriksson, 1952).

Tagging research is expensive and beset with numerous difficulties, including high and variable mortalities from the operation itself, the partial and variable efficiency of recovery of the magnets installed in meal lines at canneries and reduction plants, and the nonrandomness of the distribution of tagged members through the population during the first season of release. For a discussion of population estimates based on tagging experiments on the Pacific sardine, see Clark and Marr (1955).

3.4 Estimates based on amount of spawning

An independent estimate of population size can be derived from estimates of the amount of spawning. This estimate has the advantage of being completely independent of the commercial catch. Furtherfmore, the spawning surveys can encompass the spawning distribution of the species, and hence can be used to assess both the portion of the population that is within the range of the fishery, and that which is outside.

In order to obtain a population estimate from an egg census it is necessary also to have a reliable estimate of fecundity. There are two aspects to fecundity determinations - the number of eggs spawned per batch as related to fish weight, age or size, and the number of batches spawned per female per season. Determination of the number of eggs per batch is a straightforward problem; not so the problem of the number of batches spawned per female per year by a pelagic spawning fish (MacCregor, 1957). Until the latter problem is solved, it will not be possible to obtain a satisfactory estimate of the spawning population from egg census data. However, estimates of relative abundance can be obtained.

The reliability of estimates of number of eggs spawned depends upon many factors, including the comprehensiveness of the coverage and its frequency in time. Sette and Ahlstrom (1948) and Taft (1960) have attempted to assess the reliability of such estimates as applied to the Pacific sardine.

3.5 Estimates based on scouting surveys

Scouting surveys designed to locate and sample schools of fish throughout the distributional range of a species can furnish two important types of data : (a) information concerning the portion of the population that is outside the fishing area, and hence unavailable to the fishery (Section 4.1.2), and (b) information on the natural mortality rate of the younger fish of the population. When used in conjunction with data from the commercial catch, it is then possible to obtain an estimate of population size in which the principal parameters have been taken into account (Radovich, 1952).

4 THE PROBLEM OF AVAILABILITY

The problem of availability is not as well understood as many other facets of fishery biology. This arises, in part, because of the several quite different interpretations of the term "availability". One use of the term deals with behaviour of fish within the range of the fishery. Fish, for example, may occur at greater depths than usual, perhaps in response to a change in hydrographic conditions, and consequently be harder to locate and catch, or they may form into schools too small to be profitably fished. Other examples of this kind of availability will occur to anyone dealing with fishery problems.

The term "availability" is also applied to the portion of the total population that is within the geographic range of the fishery. Under this meaning, the total population is made up of two parts : (a) the available portion which is within the geographic area of the fishery, and (b) the unavailable portion which is physically outside the area of the fishery.

In migratory species, the portion of the population that is within the fishing area will change with the season. A population conceivably could be wholly within the range of a fishery during one season and completely outside the range during another. Obviously if this pattern pertained, the fishing would be prosecuted only during the period when the population would be fully available. More commonly, only a portion of the population will be available even during the season of the year of maximum availability, the remainder or unavailable portion of the population not entering the area of the fishery at any time during the year. The portion of the population that is available to the fishery may vary markedly from year to year, depending partly on population size, partly on the species' response to changing oceanographic conditions within its range of distribution. If the population is made up of subpopulations with different distribution, migration patterns, and physiological requirements, their relative proportions in the population can have marked effects on "availability". In a fishery that is carried on for only part of the year, such as the fishery for the Pacific sardine, the "available" population must be restricted to the portion of the population that is present within the fishing area during the fishing season. Even during this season there will be migration into and out of the area. Obviously the fraction of the population that remains in the fishing area throughout the season will be more vulnerable to fishing mortality than the portion that emigrates. The measure of availability for a season should be the average or integrated availability over the whole season. This measure would be similar to a seasonal mortality rate.

Marr (1951) discussed the problem of availability; the following definitions are based primarily on those of Marr, but behaviour-connected "availability" is separated from "availability" and given the term "vulnerability". Availability, as defined below, will have a more restricted meaning than that given by Marr.

Abundance is the absolute number of individuals in a population. Since a population is made up of pre-recruits and post-recruits, the abundance that is of relevance to the fishery is that of post-recruits.

Availability is the portion (a percentage) of the recruited population that is physically within the geographic range of the fishery during the fishing season.

Vulnerability is the accessibility of the fish within the geographic range of the fishery to the efforts of a fishery. This use of the term "vulnerability" is not equivalent to that of Ricker (1958).

Apparent abundance is the abundance as affected by both availability and vulnerability, or the absolute number of fish accessible to a fishery. Marr recommended the use of relative apparent abundance for measures of effort.

4.1 Measures of availability

4.1.1 Distribution of the spawning population

Since the inauguration of the CCOFI programme, the distribution and abundance of sardine eggs have been intensively investigated. Indirectly, the surveys also show the distribution and relative abundance of the spawning population.

During the past decade, most spawning has taken place in two areas : (a) between Point Conception, California, and Point San Juanico, off central Baja California, and (b) the Gulf of California. The sardine population in the Gulf of California, based on estimates of sardine eggs, appears to be of fairly large size, but since this stock does not appear to enter into the area of the commercial fishery, it will not be further considered.

The Pacific group has shifted its distribution markedly during the period of the CCOFI programme. During 1952 and 1953, the years with the lowest catches in the California fishery, between 97 and 99 per cent of the spawning occurred of central Baja California. In 1954 spawning had its greatest areal extent in recent years, being widespread off southern Baja California and northern Baja California, as well as off central California. The northward spread of spawning preceded the improved fishing of the 1954-55 and 1955-56 seasons. Since 1958, with warmer than usual water conditions prevailing in the eastern North Pacific, the larger part of the spawning population has been distributed off southern California, and the high availability was reflected in the catch of over 100, 000 tons in the 1958-59 season.

The fishery is not prosecuted during the spawning season, hence the relevance of "availability" measurements made during this season as measures of "availability" during the fishing season is dependent upon the fish remaining in the area of the fishery. From our knowledge of fish movements based on tagging, this assumption is warranted. However, the northward movement of fish after spawning may bring a larger percentage of the population into the range of the fishery, causing the availability estimate based on spawning distribution to be minimal.

4.1.2 Distribution of the population as determined from fish scouting surveys

Distribution of the population at the fishery season is being obtained from fish scouting surveys conducted off Baja California and California by the California Department of Fish and Game (Radovich, 1952). These surveys were initially undertaken to assess the size of each year class at approximately six months of age, but they have proven of equal value in assessing the distribution and relative abundance of fish of all ages. In most years, estimates of the relative size of the "available" and "unavailable" portions of the "recruited" population (or to be more specific, the fraction of the population off California as compared to the fraction off Baja California) have been similar to estimates based on egg surveys. When they have differed, the fish scouting surveys have shown a larger portion of the population off California. As noted above, this is in agreement with the information on seasonal movements of fish.

4.1.3 Estimates based on catch, effort and age data

The effect of availability on the catch and on mortality estimates was appreciated before the inauguration of CCOFI. There are several outstanding examples of changes in availability as it affected the California fishery. The decline in all year classes in the fishery between the 1945-46 and 1946-47 seasons was much greater than expected. Conversely, the decline in the population between the 1948-49 and 1949-50 seasons was not only less than expected, but many year classes showed the anomaly of a "negative" mortality (the 1944 through 1947 classes were taken in greater abundance in the 1949-50 season than in the 1948-49 season). The difference in numbers of fish of all year classes taken in the 1954-55 as compared to the

1953-54 season furnished the most outstanding example of the effects of availability on the catch. The information is given in the following Table.

Table II

YEAR CLASS COMPOSITION OF THE COMMERCIAL CATCH OF SARDINES OFF CALIFORNIA IN 1953-54 AND 1954-55 SEASONS (in millions of fish)

Year class	Number of fish taken in 1953-54 catch	Number of fish taken in 1954-55 catch
1952	1.5	174.0
1951	0.6	194.8
1950	4.2	57.4
1949	3.7	35.0
1948	7.0	54.9
1947	2.3	5.0

The effort as determined by Clark (1956) was about half as great in the 1953-54 season as in the 1954-55 season; the potential effort was as great. The average lunar month catch in the 1953-54 season was 10.7 tons; in the 1954-55 season it was 145.2 tons.

Widrig (1954) has dealt at some length with the effects of varying levels of availability on the sardine catch. In his method of determining the availability level, one season in a series is taken as a reference year and assigned the value of 100; the availability level in the other seasons is expressed as a fraction of this. Estimates of availability were derived for several possible rates of natural mortality. With an instantaneous natural mortality rate of 0.2, the 1946-47 season had an availability level of 28, as compared to the level of 100 in the reference season (1944-45); the 1948-49 season had an availability level of 22; the 1949-50 season 79. Widrig did not deal with the 1953-54 and 1954-55 seasons.

Although fluctuating levels of availability are now recognized as an important cause for fluctuations in the catch of Pacific sardine, its effect may be more conspicuous in the sardine fishery than in some others. The problem is barely considered by Beverton and Holt (1957), and the recent standard terminology and notation for fishery dynamics (Holt et al., 1959) does not include it.

5 FISHING EFFORT

5.1 Catch-per-unit-of-effort

Fluctuations in the catch may reflect differing amounts of effort expended in its capture,

as well as variations in the size of the population or the portion that is available to the fishery. The catch-per-unit-of-effort has been devised to measure changes in effort.

California effort data are available from the 1932-33 season. Prior to this season, according to Clark (1939), the supply exceeded the demands of the industry to such an extent that boats were on rigid limits; any increase in effort merely reflected increasing industry demands rather than fluctuations in abundance or availability. During most years prior to 1932, the fishery was carried out by lampara nets and lampara boats. By 1932, the purse seine was the dominant gear, operated from purse seine vessels.

The Pacific Northwest fishery has been a day fishery, the California a night fishery. Schools of fish are detected off California by their luminescence as they move through the water. The luminescence can be seen only at night during the dark of the moon, and fishing is limited to these times. Because of the relation of fishing to the moon, the effort has been reported as either the catch per lunar week, or per lunar month. All recent papers on effort have reported on the average lunar month catch.

The most detailed study of effort is that of Silliman and Clark (1945). Adjustments were made in effort data for effects of weather and catch limits, but had so little effect on the results that they were subsequently abandoned. These adjustments were considered necessary, inasmuch as the only information available for each vessel was its landings. Log books have not been systematically used by the sardine fishermen, so information is not available concerning the number of nights actually fished per week or per month. For limited periods of time, such as the war seasons of 1943-44 through 1945-46, the day by day activity of each vessel is known, but these data have not been used in determinations of effort.

Continuity is achieved over the years by comparing a vessel with its own performance in succeeding seasons. Two effort determinations are derived for each season, one based on linkages with the preceding season, the other on linkages with the succeeding season.

The purse seine fleet does not fish solely on the Pacific sardine even during the sardine season. The sardine is usually the preferred species, but the seiners also take Pacific mackerel, jack mackerel and sometimes anchovy. Catches of other species are not included in catch-per-unit-of-effort determinations. For this reason, effort determined on sardine landings alone must be accepted with certain reservations. The papers by Clark and Daugherty (1950, 1952) and Clark (1956) contain summaries of effort data for California ports between 1932-33 and 1954-55. Effort data for subsequent seasons are not yet available. Eventually, effort based on total landings of all species by the purse seine fleet during the sardine season should be derived.

5.2 Yield-per-recruit

Beverton (1953), and Beverton and Holt (1957), have separated the population of a fish into two groups : pre-recruits and post-recruits, and have further divided the post-recruit phase into pre-exploited and exploited components. Fish are considered to be recruited when they enter the area where fishing is in progress, and became available to fishing gear. They enter the exploited phase when they are retained by the fishing gear.

These are useful distinctions in a fishery where changes in mesh size can alter the age at first capture - and thus influence the eumetric yield.

The distinctions have no relevance to the Pacific sardine fishery. Only a small portion of a year class is "catchable" as one-year-old fish, a larger but still incomplete portion as two-year-olds, and the class is not fully "exploited" until three years of age. Younger fish apparently have a different schooling behaviour than older fish.

Yield-per-recruit studies, on the other hand, have shown that the highest yield can be obtained under the usual fishing and natural mortality coefficients from an age at first capture of one year at San Pedro, and an age at first capture of two years at central California and Pacific Northwest fishing areas. The difference between ports is due to different growth patterns of the sardines in the various fishing areas (Phillips, 1948; Felin, 1954). The yield-per-recruit relation in the present fishery is probably as advantageous as can be obtained, taking into account the age-connected behaviour of the fish, size preferences of the industry, the fluctuations in size of year classes and varying availability. No advantage could be derived by changing the mesh size of the round haul nets used in the capture of sardines.

6 FLUCTUATIONS AND THE FISHERY

The catch of the Pacific sardine has had marked fluctuations in amount - from a high of 736,000 tons in 1936-37 to a low of approximately 10,000 tons in the 1953-54 season. The catch reflects the interaction of population abundance, population availability and fishing effort. What part did the fishery play in "causing" these fluctuations?

6.1 Effect of fishery on availability

The fishery can affect availability by reducing through fishing mortality the portion of the population that is accessible to the fishery. Unless the total population redistributes itself more or less randomly throughout the fished and non-fished portions of its range, a progressive reduction in the available portion could take place. If there is no redistribution of fish, then the non-available portion of the population could be considered a separate stock, and dismissed from consideration. However, this would be likely to occur only in a fish with sedentary habits and not in a strongly migrating species, such as the Pacific sardine. The mor likely occurrence in the case of the sardine would be a partial and variable redistribution of fish. Such a redistribution would be in accord with both the evidence of movements from tagging experiments (Clark and Janssen, 1945), and of population heterogeneity (Felin, 1954).

Considered from another viewpoint, the problem of availability is an accident of geography (California fishermen do not fish off Baja California for sardines, and vice versa) that has been superimposed on the distribution of a fish population that responds to hydrographic rather than geographic boundaries.

6.2 Effect of the fishery on population size

This is without a doubt the most controversial subject in fishery biology. Opinions range from that of Huntsman (1953) that "there seems to be no good basis for restricting fishing

in order to increase the long-term yield", to the hopeful statement of Russel (1939) that "We may safely draw the conclusion ..... that there must be for every stock an optimum rate of fishing, which will give the maximum steady yield (subject, of course, to variations due to natural fluctuations which, however, cancel out over a period of years, and to variation in growth rate)".

One line of investigation of the influence of the fishery on the stock centres around a density dependent rate of natural increase - an idea particularly championed by Graham (1935, 1939), and postulated for the Pacific sardine by Sette (1943) and Schaefer (1954a and b).

Schaefer (1954a) notes : " Large-scale fluctuations in fish population and catch can arise as a result of the forces of growth of the fish population and growth of the intensity of fishing, with all other conditions constant". Each population has a single maximum or optimum stock, corresponding to the inflection point of the growth curve. The model proposed by Schaefer is designed to take advantage of the optimal rate of increase of a population.

Unfortunately, most authors who have postulated taking advantage of the optimal rate of increase have considered only the integrated effect of all the factors that influence the dynamics of a population, and not the importance of individual components. The components, presumably, would be fourfold : (a) the rate of increase in growth, (b) the rate of natural deaths, (c) fecundity, and (d) recruitment.

Increase in weight of recruited individuals is partly a function of age (young fish have a greater increase in weight per unit time than old fish), partly a function of population density (intraspecific competition). A reduction in intraspecific competition would result in increased growth because of the greater amount of food available per individual.

Various investigators have shown an increase in natural mortality with age of the recruited stock (for example, Tester, 1955). The optimal population being composed principally of younger individuals should have a lesser rate of natural mortality than a larger stock size in which older individuals were more dominant.

The favourable effects on fecundity, if they occur, would be hard to substantiate because of the difficulty of measuring fecundity with sufficient precision. Favourable effects on recruitment would result only if success of recruitment were density dependent, with the highest recruitment at or near the optimal stock size. For recruitment to be density dependent, the tacit assumption must be made that intrinsic factors are more important in determining success of survival of year classes than extrinsic influences. This is the critical assumption in the model.

Even a cursory examination of the data bearing on the relation between year class size and spawning stock size for the Pacific sardine reveals that the effects of extrinsic factors must be large as compared to intrinsic ones. If there is a relation between spawning stock size and the size of the resulting year class, it is masked by the more dominating environmental influences.

Table III shows a comparison between the year classes over a 15-year period (1939-53) as against the relevant spawning population. The size of the spawning population in each year

s based on the virtual population estimate of fish two years of age and older. Year class size s based on the total contribution of each class to the fishery during the life span. The values ıre influenced by varying availability.

The largest year class in the series, the 1939 class, contributed nearly 60 times as nany fish to the commercial catch as the 1950 class, yet the estimated size of the spawning ɔopulation in 1939 was less than twice as large as in 1950. Survival during 1949 and 1950 can ɔnly be described as disastrously low.

Table III

COMPARISON OF YEAR CLASS SIZE vs SPAWNING POPULATION SIZE IN THE PACIFIC SARDINE (in billions of fish)

Year	Spawning population	Year class	Ratio of year class / Spawning population
1939	6.77	7.52	1.11
1940	8.40	3.50	0.42
1941	11.64	2.20	0.19
1942	9.10	2.80	0.31
1943	6.96	1.85	0.27
1944	5.80	1.13	0.19
1945	3.58	1.56	0.44
1946	1.75	2.24	1.28
1947	1.36	3.13	2.30
1948	2.70	2.21	0.82
1949	4.28	0.14	0.03
1950	3.66	0.13	0.04
1951	1.20	0.38	0.32
1952	0.37	0.58	1.57
1953	0.50	0.18	0.36

6.3 Fish classified according to importance of intrinsic versus extrinsic influences in recruitment

This brings up a subject that is in need of critical appraisal - the relative importance of extrinsic versus intrinsic influences in the success of recruitment of the major commercial species. The writer believes that important food fishes can be placed into at least three groups with regard to the importance of intrinsic versus extrinsic influences in recruitment:

Group 1 : Intrinsic factors predominate. Variations in level of recruitment moderate, or buffering action of a number of year classes in spawning population dampens the effect of fluctuations;

Group 2 : Intrinsic factors predominate at times, extrinsic influences at other times. Variation in level of recruitment greater than in (1), less than in (3);

Group 3 : Extrinsic factors so predominant that intrinsic influences are masked. Variation in level of recruitment marked. Number of year classes in spawning population usually few.

The plaice, halibut and yellowfin tuna may fall in Group 1; such species as the cod and haddock in Group 2, and pelagic schooling fishes such as the Pacific, Japanese, and European sardines in Group 3.

If this classification is at all valid, it brings to light basic implications in fishery management. Species in Group 1 would be amenable to management, especially that directed toward obtaining the optimal catch; species in Group 2 less amenable; while species in Group 3 would be intractable.

6.4 Models

Beverton (1953) has stated the problem of fishery management as follows : "Our basic problem is to gain an understanding of the mechanisms which enable a fishery to reach a steady state and of the factors contributing to it, with special reference to the factors which are potentially within man's power to control, namely the amount and kind of fishing activity. The first objective is to determine the balance which is most advantageous to man, and to define the regulative measures which are required to achieve it."

He continues : "The only satisfactory method of tackling this problem in the North Sea fisheries - and probably in most others - is to set up a theoretical model of an exploited fish population which represents as faithfully as possible the fishery in question."

Several authors have set up models or procedures of investigation applicable to the Pacific sardine, especially Schaefer (1954a and b), and Sette (1943). These are stimulating papers, and if they do not satisfy all investigators, it is because of the simplifying assumptions that are inherent in present models.

A model that will adequately take into account the peculiar features of a pelagic marine schooling fish, such as the Pacific sardine, is a basic objective of our research. The model must take into account the very marked fluctuations in survival of year classes that occur in such populations. It must take into account the problem of varying availability. Our fishery does not encompass the distributional range of the Pacific sardine, but only a portion, and in recent years a markedly variable portion of the population is within the area of the fishery. Adequate measures of natural mortality are among our urgent needs. With such information we could eliminate from models the assumption that natural mortality is constant from season to season, or similar for the sub-groups that comprise the population of the Pacific sardine.

This paper has not answered the basic question - what is the relation of the fishery to fluctuations in abundance of sardine-like fishes? It has tried to point out some of the problems that make a categorical answer difficult if not impossible at our present state of knowledge. If the writer has limited his observations mostly to the fishery for the Pacific sardine, it is because it is best known to him, and its problems appear to be typical of the fisheries for other sardines.

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FB/SI7
SAST - Sardine

SYNOPSIS
ON THE BIOLOGY
OF THE PACIFIC SARDINE
(Sardinops caerulea)

Prepared by

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FISHERIES DIVISION, BIOLOGY BRANCH
FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, 1960

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SYNOPSIS ON THE BIOLOGY OF THE PACIFIC SARDINE
(Sardinops caerulea)

Exposé synoptique sur la biologie de la sardine du Pacifique (Sardinops caerulea)

Sinopsis sobre la biología de la sardina del Pacifico (Sardinops caerulea)

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PURPOSE OF THIS SERIES

This is one of a series of synopses of biological data concerning species of aquatic organisms of economic importance. The primary purpose of this series is to make existing information readily available to fishery scientists, according to a standard pattern, and by so doing also to draw attention to gaps in knowledge. It is hoped that synopses in this series will be useful to scientists initiating investigations of the species concerned or of related ones; as a means of exchange of knowledge among those already working on the species, and as the basis for comparative study of fishery resources.

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SAST - Sardine

SYNOPSIS ON THE BIOLOGY OF THE PACIFIC SARDINE
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1 IDENTITY

1.1 Taxonomy

1.1.1 Definition

The Pacific sardine is a pelagic marine schooling fish inhabiting temperate waters of the eastern North Pacific. It reaches a maximum size of approximately 300 mm LS. The usual size of fish taken by the commercial fishery for canning (and reduction) is between 150 and 250 mm LS. The Pacific sardine is similar in size and general appearance to the European pilchard.

The Pacific sardine, Sardinops caerulea (Girard) 1854, is closely allied to four other species of sardines :

Sardinops sagax (Jenyns) 1842 . . . . . Chilean

Sardinops melanosticta (Temminck and Schlegel) 1846 . . . Japanese

Sardinops ocellata (Pappé) 1853 . . . . . South African

Sardinops neopilchardus (Steindachner) 1879 . . . . . Australian

These species are so similar as to be doubtfully distinct. It has been proposed by Svetovidov (1952) that Sardinops caerulea, S. melanosticta, S. ocellata and S. neopilchardus be considered subspecies of Sardinops sagax. A morphometric and meristic study is being made on the five species of Sardinops at the Scripps Institution of Oceanography; pending its completion, the specific name caerulea will be retained for the Pacific sardine. The conclusions now permissible from this study indicate that all currently recognized species will be synonymized under the name Sardinops sagax (Jenyns); only Sardinops neopilchardus from Australia and New Zealand appears to merit subspecific rank.

Differences between the European pilchard and the Pacific sardine have been pointed out by Regan (1916), Thompson (1926), and Hubbs (1929), among others. Two of the differences that led Hubbs to create the genus Sardinops were in scale arrangement and gill raker structures The scales of each alternate row in Sardina pilchardus so nearly overlap that the apparent number of rows is only about half the true number; the overlap is less marked in Sardinops caerulea, and the apparent number of scale rows is equal to the true number. The gill rakers on the lower limb of Sardinops caerulea, unlike the European sardine, become gradually and markedly shortened toward the angles of the arch; the rakers on the upper limb fold over those of the lower limb near the angle in the Pacific sardine, while they do not in the European species; gill rakers also differ between the two species in number at comparable sizes.

1.1.2 Description

The characters of the genus Sardinops as defined by Hubbs (1929) also serve to characterize Sardinops caerulea:

> "Clupeidea with the upper jaw not notably notched on the mid-line; the gill rakers of the upper limb folded over those of the lower limb, which become markedly and progressively shortened toward the angle; carina of glossohyal not denticulate; no

bilobed dermal flap on shoulder-girdle; opercle with strong and markedly oblique ridges; preopercular edge strongly sloping; interopercle widely exposed behind preopercle; scale rows regularly spaced, the lateral scales all with subequal exposed areas; radii on the scales nearly vertical, and paired on each side of median line, keels on vertical scutes weak; last two rays of dorsal and anal fins somewhat enlarged; a row of dark spots typically developed on upper sides behind head."

1.2 Nomenclature

1.2.1 Valid scientific name

Probably Sardinops sagax (Jenyns) 1846. For the present, however, the name Sardinops caerulea (Girard) 1854 is retained for the species off western North America. Only a synonymy pertinent to Sardinops caerulea is given below.

1.2.2 Synonyms

Sardinops caerulea (Girard). Hubbs, Carl L., 1929. Proc. Calif. Acad. Sci., vol. 28, No. II, pp. 261-265

Maletta caerulea (Girard), 1854. Proc. Acad. Nat. Sci., Phila., vol. 7, pp 138-139

Alausa californica Gill, T.N., 1862. Proc. Acad. Nat. Sci. Phila., (for 1861), p. 33

Clupea sagax Jenyns, 1842 in Jordan and Gilbert, 1881. Proc. U.S. Nat. Mus. (for 1880), vol. 3, p. 30

Clupanadon caeruleus Gilbert, C.H., 1899. U.S. Comm. Fish Rept. (for 1898), p. 25

Sardinella caerulea Hubbs, Carl L., Copeia, 1917, no. 43, p. 38

Sardina caerulea Jordan D.S., 1917, Copeia, 1917, no. 49, pp. 85-89

Sardinia caerulea Dill, D.B., 1921. Jour. Biol. Chem., vol. 48, No. 1, pp. 93-103

1.2.3 Standard common names, vernacular names

The standard common name of Sardinops caerulea is Pacific sardine. A frequently used name, particularly in Canada, is Pacific pilchard. For many years the name California sardine was in rather general use, but this name has been dropped in favor of Pacific sardine.

1.3 General variability

1.3.1 Subspecific fragmentation (races, varieties, hybrids)

The problem of subpopulations (or races) is one of the major lines of investigation of the Pacific sardine. Heterogeneity within the distribution of Sardinops caerulea has been clearly demonstrated (Phillips, 1948; Felin, 1954). Fish collected off British Columbia are larger for the same age, and have a different growth pattern from fish collected off San Pedro. There are differences in size and age composition of the landings at closely allied ports, as, for example, between San Pedro (California) and Ensenada (Baja California). This was particularly evident during the 1958-59 sardine season.

Large-scale tagging experiments conducted by the California Department of Fish and Game and other groups between 1935 and 1942, with recoveries continuing for a number of years subsequently, showed extensive movements of sardines between the various fishing areas.

Vertebral studies conducted by Clark (1947) over a period of years, showed the following differences within the distributional range of Sardinops caerulea :

Table I

Sardinops caerulea : VERTEBRAL COUNT (Clark, 1947)

Locality	Average number of vertebrae	Number of fish examined
Alaska to U.S.A. - Mexico boundary	51.718	48, 182
Northern Baja California, south to Point San Eugenio	51.585	4, 289
Point San Eugenio, Baja California, to Cape San Lucas	51.354	5, 573
Gulf of California	51.037	1, 557

These studies are further evidence of heterogeneity within the distribution of Sardinops caerulea, but they do not necessarily show the existence of more than one population. From central Baja California south, however, the mean number of vertebrae decreases rapidly with latitude, indicating that the stocks in these waters are more or less distinct from those of the north.

McHugh (PhD thesis) gives data on the number of vertebrae in postlarval sardines from off California and Baja California, which show the seasonal differences that are obtained off Baja California :

Table II

NUMBER OF VERTEBRAE IN POSTLARVAL SARDINES OFF CALIFORNIA AND BAJA CALIFORNIA (McHugh)

Areas and seasons	Mean	$S(x-x)^2$	Number
Northern California - summer	51.88	7.77	17
Southern California - summer	51.73	43.28	109
Northern Baja California - spring	51.79	27.12	68
summer	51.17	16.61	46
Southern Baja California - spring	51.54	95.14	278
- summer	51.21	62.25	192

The seasonal means for both northern and southern Baja California show highly significant heterogeneity, which is undoubtedly related to spawning temperatures during the two seasons.

The seasonal difference in mean number of vertebrae off northern Baja California is nearly as large as the extreme difference between areas as reported by Clark.

One of the principal lines of research in the California Cooperative Oceanic Fisheries Investigations (CCOFI) has been the determination of the distribution and abundance of sardine spawning. These surveys have shown that there are three groups of spawning sardines that either temporally or areally are fairly distinct and might possibly constitute separate subpopulations or races. These three groups are : (1) the main spawning group of sardines off California and Baja California, spawning between January and June at water temperatures between 13° and 17°C; (2) an off-season spawning group off central Baja California, located principally in Sebastian Viscaino Bay, and spawning at temperatures that average about 3°C higher than during the main spawning period; and (3) sardines in the Gulf of California.

1.3.2 Genetic data (chromosome number, protein specificity)

Genetic studies of the Pacific sardine using immunologic techniques have been carried out with a view toward using the erythrocyte antigens as genetic indicators. Three blood systems have been discovered in the sardine, designated as the A, B, and C systems (Sprague, unpublished data).

The A system, the first system distinguished in the sardine, is believed to be a three allele (A_1 - A_2 - a), four phenotype (A_1 - A_1A_2 - A_2 - a) system.

The B system is characterized by three serologic reaction patterns. There are three phenotypes known which are designated B, BG and I, and at least three alleles (B^I - B^G - B^B).

The C system is a two allele (C - c), two phenotype (C - cc) system. Samples tested are either positive or negative with the C reagent.

Sardines tested from southern California and various localities off Baja California have shown no significant differences in the proportion of phenotypes in the B or C systems. However, a group of sardines from off central California tested in July 1959 were significantly different in the proportion of positive and negative individuals of the C system. This is the first evidence that there may be separate genetic groups in the Pacific sardine. Sardines from other areas have yet to be tested - especially fish from the Pacific Northwest and from the Gulf of California.

Other types of genetic studies have not been made on the Pacific sardine. The number of chromosomes is not known.

The only studies that have been made on protein specificity are preliminary ones using paper chromatographic techniques. A study involving variation in the free amino acid complex of sardine muscle tissue was made by Farris (1958). This experiment was designed to show the effect of diet on two primary amination products, aspartic acid and alanine. Their presence was shown to vary inversely with the fatness of the fish, i.e. a high proportion of starved fish contained aspartic acid and alanine in the muscle tissue, while a high proportion of the well-fed fish did not. Fish fed on a high carbohydrate diet were more likely to have aspartic acid in the muscle than fish fed on a diet high in protein. The experiment demonstrated that variation can be caused in muscle-free amino acids by diet, hence chromatographic studies must distinguish between genetically controlled differences and those which are induced by environment.

2 DISTRIBUTION

2.1 Delimitation of the total area of distribution and ecological characterization of this area

The Pacific sardine inhabits the Pacific coastal waters of North America from southern Alaska to Cape San Lucas and the Gulf of California. In the northern portion of the range its occurrence is seasonal. In recent years, the center of maximum abundance has been between Point Conception, California, and Point San Eugenio, off central Baja California.

The Pacific sardine (except in the Gulf of California) occurs in waters whose dominant feature is the California Current.

The California Current is an eastern limb of the large clockwise circulation in the North Pacific. It is low in salt content and in temperature. It derives its characteristics from the warm and saline waters of the Kuroshio Current, the cold and less saline waters of the Oyashio Current, and from precipitation and cooling which takes place in this water mass as it moves across the North Pacific Ocean, between latitudes 40° and 45°N. Near the coast of North America the current splits into two parts, one turning northward into the Gulf of Alaska, the other southward to become the California Current. The water which turns northward is warmer than that offshore at the same latitude; that which turns southward is cooler than that offshore.

Upwelling occurs at a number of places along the extent of the California Current. Through the agency of northwesterly winds, the upper layers of water are pushed offshore and are replaced by deeper, colder waters which normally lie below the pycnocline. These waters are rich in inorganic phosphate-phosphorus and other nutrients; this enrichment accounts in part for the fairly high productivity along Pacific coast states. In the southern part of the region (25° - 32°N latitude) upwelling occurs mainly in the spring period; one consequence is an increased seasonal range of temperatures above that of offshore waters in the same latitude. North of 35°N latitude upwelling occurs in the summer months and reduces the seasonal range of temperatures below that of offshore regions.

A northward-flowing counter-current occurs in the winter months and carries warm water northward. A curious result of the winter counter-current and summer upwelling off central and northern California is that midsummer water temperatures are often lower than those in December or January.

The Gulf of California has a narrow but deep connection with offshore waters. Because it is enclosed on three sides and lies in a region of low rainfall, its salinities are much higher than those of the California Current region. Upwelling has been observed in the Gulf, but at different times of the year, and to a lesser extent than on the Pacific coast of Baja California. In winter the temperatures are much like those of the ocean, but in summer the temperatures are much higher. The seasonal range in the northern part of the Gulf is over twice that of eastern Pacific Ocean water at the same latitude.

Our chief means of determining distribution of sardines within the Gulf has been spawning (egg and larval) surveys. Sardines have been found to spawn over much of the Gulf, although the heaviest concentrations of eggs have been obtained in the central part. Spawning occurs during the winter period.

2.2 Differential distribution

2.2.1 Areas occupied by eggs, larvae and other junior stages : annual variations in these patterns, and seasonal variations for stages persisting over two or more seasons. Areas occupied by adult stages; seasonal and annual variations of these

Although sardine spawning has been sampled as far north as Oregon, and young fish from British Columbia waters, these occurrences appear to have been sporadic. Sardine spawning may have occurred fairly regularly off central California prior to the collapse of the sardine fishery in that area; in recent years it has been sporadic and small in amount. Since the inauguration of the CCOFI, sardine spawning in Pacific waters has been mostly confined to the area between Point Conception, California, and Magdalena Bay, Baja California. Even within this region, the distribution of spawning has been markedly different in different years. Hence, in a strict sense there is no area to which sardines return season after season to spawn. Sardines appear to respond to their oceanographic climate rather than to geographically-fixed reference points during the spawning season.

The annual distribution of sardine spawning from 1949 through 1956 has been given by Ahlstrom (1954, 1959). During 1952 and 1953, most sardine spawning occurred off central Baja California. Sardine spawning had its greatest areal extent in 1954, when spawning was widespread off southern California and northern Baja California as well as off central Baja California. A similar distribution of spawning occurred in 1955 and 1956, although somewhat more restricted in areal extent.

Sardine larvae have been found to have a somewhat wider distribution than the eggs, and to have their distribution displaced somewhat to the south of the eggs, undoubtedly because the current flow in the region of the California Current is predominantly to the south.

The distribution of juveniles is not as well known as that of eggs or larvae, partly because the juveniles are more difficult to sample. They are found near shore in shallow water (10 fa.) and this region is believed to be their principal habitat. However, juvenile sardines have been taken in albacore stomachs at considerable distances offshore (100 miles or more). Except for these isolated observations, nothing is known of their offshore distribution.

Juveniles in inshore waters have been surveyed annually since 1950 by the California Department of Fish and Game, hence there is a considerable body of information on the alongshore distribution of juveniles. Juveniles are usually distributed south of the main spawning area.

In recent years, juveniles were common off southern California only in 1957. They have been taken in various localities off northern and central Baja California but consistently only in the Sebastian Viscaino Bay area.

After spawning offshore in the spring, adult sardines move inshore during July and August. There are two areas in which sardines seem to congregate after spawning. One such area is in the channel between Anacapa and Santa Cruz Islands and the mainland (off southern California). Sardine catches are usually heavier in this area during the first part of the season (which now commences on 1 September, but previous to 1957 opened on 1 October). From the Santa Barbara Channel Island area, sardines disperse along the coast, generally southward. They usually are found within 20 miles of the shore, except for their occurrence around the islands.

The other area in which sardines appear to concentrate is the lower portion of Sebastian Viscaino Bay, off central Baja California.

During years when spawning is inshore there seems to be less of a tendency for massing in the areas specified.

2.3 Behaviouristic and ecological determinants of the general limits of distribution and of the variations of these limits and of differential distribution

The results of tagging experiments (Clark and Janssen, 1945) have shown that there are extensive movements of the sardine which are partly age connected. Fish move northward in the summer and southward again in the fall - the northward extension being greater with each year of age. The northward movement appears to be primarily a feeding migration, the southward movement a return to spawning grounds off southern and central California.

Temperature appears to be an important determinant of sardine spawning distributions. The threshhold temperature for spawning seems to be about 13°C. Most spawning occurs at temperatures between 13° and 17°C, with perhaps optimum conditions between 15° and 16°C. The time of year when favorable temperatures occur, as well as the length of time that they persist, have an influence on the areal and seasonal distributions of spawning (see 3.1.6).

A rather good relation has been observed in recent years between the distribution of sardine spawning during the spring months and the availability of fish to the commercial catch during the following fishing season. When negligible spawning occurred off California in 1952 and 1953, the catches were the lowest on record (3,000 to 5,000 tons). The northward expansion of spawning into the southern California area in 1954 was followed by a fairly marked increase in catch - 67,000 tons in the 1954-55 season, and 73,000 tons in the 1955-56 season.

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.1.2 Maturity (age and size)

The small, in situ ova of the sardine are transparent, with the nucleus plainly visible. They contain no yolk material up to a diameter of about 0.20 mm. Large ovarian eggs contain yolk which makes them opaque and obscures the nucleus. Sardine ova continue to be opaque during maturation until immediately before spawning, when they again become translucent. The diameter of the yolk portion of the egg of the sardine at spawning is 0.85 - 0.90 mm.

Relation of maturity to fish length is shown in Table III. The data, taken from MacGregor (1957), are based on collections during 21-28 February, 1946 and cover the period when the largest percentage of females were maturing.

Table III

STATE OF MATURITY OF FEMALES SAMPLED AT SAN PEDRO BETWEEN 21 AND 28 FEBRUARY 1946

LS (mm)	Number examined	Percentage with yolked ova	Percentage with ova > 0.40 mm
140-149	1	0	0
150-159	24	17	0
160-169	22	32	0
170-179	2	100	50
180-189	10	100	70
190-199	20	100	100
200-209	9	100	100
210-219	9	100	100
220-229	3	100	100
230-259	3	100	100
Total	103		

In the latter part of February 1946, all females over 170 mm were maturing and most had larger ova (1°C ova > 0.40 mm).

During 1958, a year when water temperatures in the upper mixed layer off California and Baja California averaged 1° to 2°C above the average of the preceding eight years, sardines of much smaller size were maturing in collections obtained from the fishery at Ensenada, Baja California (Table IV).

Table IV

STATE OF MATURITY OF FEMALES SAMPLED AT ENSENADA, BAJA CALIFORNIA, BETWEEN 7 AND 12 MARCH 1958 1/

LS (mm)	Number examined	Percentage with yolked ova	Percentage with ova > 0.40 mm
110-119	22	18	5
120-129	96	55	5
130-139	24	79	8
140-149	19	100	68
150-159	8	100	100

1/ Only fish under 160 mm are noted.

Previous to 1958, the smallest sardine with yolked ova measured 145 mm and was obtained from the extreme southern part of the range (Cape San Lucas)

Table V

BREAKDOWN BY AGE FOR SAN PEDRO COLLECTIONS 21-27 FEBRUARY 1946 (MacGregor, 1957)

Age	Year class	Number examined	Percentage with yolked ova	Percentage with ova >0.40 mm
1	1945	43	28	0
2	1944	29	100	83
3	1943	17	100	100
4	1942	6	100	100
5-9	1941-1937	5	100	100

In 1958, a higher percentage of one-year-old fish sampled at Ensenada during March and April contained yolked eggs, and some individuals had ova in advanced stages of development. One can conclude from the above that the majority of sardines spawn at age two, and that under favorable environmental conditions a portion of the one-year-old fish will also spawn.

3.1.3 Mating (monogamous, polygamous, promiscuous)

The Pacific sardine is a pelagic marine spawning fish. The eggs are fertilized externally after being shed into the water. The sexes retain their identity throughout their life. There is no mating in a strict sence, and no parental care of eggs or young.

3.1.5 Fecundity

Fecundity studies on the Pacific sardine have been made by Clark (1934) and MacGregor (1957).

3.1.6 Spawning

- Spawning seasons (beginning, end, peak)

The distribution of spawning of the Pacific sardine, based on collections of eggs and larvae, has been as thoroughly investigated, both areally and temporally, as that of any other pelagic marine schooling fish. The season of spawning differs in different parts of the known spawning range of the sardine.

In the southern part of its range, off central and southern Baja California, spawning occurs throughout the year with peaks in the winter and summer months. Off southern California, spawning was mostly confined to the spring months (April-June) during 1950 through 1956. With the advent of warmer water conditions, which have lasted from 1957 to date (July 1959), spawning has occurred earlier in the year off southern California and continued over a longer period of time - January through July, with some spawning at other seasons. Spawning to the north of Point Conception, which in recent years has been sporadic, has taken place from May through August (mostly in June). In the ten year period, 1949-58, spawning occurred to the north of Point Conception during five years: 1949, 1950, 1954, 1957 and 1958; in only one season, 1949, were more than negligible numbers of eggs and larvae obtained from waters of this region.

The spawning season in the Gulf of California has not been delimited completely, since there have been only eight cruises in this area. Considerable spawning has been sampled during the months of February and April, but sardine spawning appears to be lacking during the summer and fall months. Temperatures during the summer and fall in the Gulf of California are much higher than on the outer coast of Baja California in the same latitudes, and the lack of spawning in the Gulf during these seasons is undoubtedly associated with unfavorably high water temperatures. The size of the population in the Gulf appears to be fairly large.

- Number of spawnings per year, frequency

MacGregor (1957) found that the number of eggs produced per batch was more closely related to fish weight than to length or age. In fact, the number of eggs produced is almost directly proportional to fish weight.

The estimated number of ovarian ova present in the most advanced group of yolked ova in a sardine 200 mm in length is 26.8 thousand. The rate of increase or decrease in the estimated number of ova is 5.14 thousands per increase or decrease of 10 mm in length. There is considerable variation in the number of ova produced by individual fish at any given length. The standard error of estimate of Y for 10 mm length intervals using the formula $Y = a+bX$ is 8.76 thousands of ova.

The problem of the number of batches spawned per female per year is much more difficult to solve than that of the number of eggs spawned per batch. The data presented by Clark (1934) and MacGregor (1957) are not in agreement

A sardine ovary in an advanced state of maturity always contains a wide range of sizes of yolked ova and often several well defined size modes.

Workers have agreed that the largest mode contains the eggs that will be spawned in one batch. Clark found that this largest size group represented only one egg to four in less advanced stages of development in the early part of the season, but that the proportion changed to one to two in the later part of the season. She postulated that the decrease in proportions resulted from successive maturing of batches of eggs and that the evidence supported three batches having been matured. The smaller yolked eggs remaining in the ovary at the end of the spawning season presumably are resorbed.

MacGregor (1957) has found a much smaller proportion of eggs in less advanced stages of development. He found one advanced to about 1.5 less advanced ova in the average ovary early in the season, with no marked change in proportion during the season. He could find no clearcut evidence in support of multiple spawnings. An experimental approach to this problem is badly needed.

- Spawning time of day

Based on the time of collection of precleavage sardine eggs, sardine spawning occurs mostly between 8 pm and midnight (Ahlstrom, 1943).

- Induction of spawning, artificial fertilization

Pacific sardines held in aquaria do not mature and spawn. Spawning sardines in nature are difficult to collect. Sardine eggs have been artificially fertilized on one occasion only (Miller, 1952).

3.1.7 Spawning grounds

- Oceanic (surface, bottom)

Sardine spawning occurs in the open ocean, usually over deep water. Ova and milt are shed free in the water. Success of fertilization appears to be very high, since unfertilized eggs are seldom obtained. Sardine eggs are found only in the upper mixed layer, and upper portion of the thermocline, between the surface and approximately 100 m.

The Pacific sardine is known to spawn from Oregon south to Cape San Lucas, Baja California, and throughout most of the Gulf of California. The chief spawning areas other than the Gulf are off southern California and central Baja California.

As noted in section 2.2, the relative abundance, distribution and extent of spawning in the spawning areas have varied rather markedly during the decade 1949-58.

3.1.8 Egg: structure, size, hatching type, parasites and predators

The sardine egg at spawning is approximately 1.0 to 1.1 mm in diameter, but the outer membrane soon expands to a diameter of approximately 1.7 mm. The spherical yolk mass does not increase in size after spawning, and averages about 0.9 mm in diameter. However, the width of the perivitelline space increases from less than 0.1 mm at spawning to approximately 0.4 mm after the expansion of the unsculptured, outer shell membrane.

Embryonic development requires approximately three days at 15°C. From a study of the influence of temperature on the rate of development of sardine eggs in nature, it was determined that the time required for embryonic development increases by about 7 per cent for each 0.5°C decrease in temperature (Ahlstrom, 1943).

One batch of sardine eggs collected off southern California in 1957 were infected by a fungus, with mycelia extending throughout the perivitelline space. The presence of bacterial investations has not been determined. However, a portion of sardine eggs are often stunted and misshapen and are recorded as "abnormal". Such abnormalities can result from injury during collection, as Rollefsen (1930) demonstrated for cod eggs. Some abnormalities, however, may result from a diseased condition of the eggs.

Predators include other members of the plankton community - especially chaetognaths, siphonophores, jellyfish, ctenophores, and filter-feeding nekton including juvenile and adult sardines. Predation during the embryonic period does not appear to be high, probably because the eggs are dispersed and translucent, hence difficult to see. Since they are relatively inactive they probably do not attract predators through motion.

3.2 Larval history

3.2.1 Account of embryonic and juvenile life (prelarva, larva, postlarva, juvenile)

Sardine larvae are pelagic, free-swimming organisms living in the upper mixed layer. (The inclusive term "larva" is preferred by us to the terms "prolarva" and "postlarva"). The sardine larva is approximately 3 mm long at hatching, about 4.5 to 5.0 mm long at the completion of yolk absorption, approximately 25 mm long at the beginning of metamorphosis, and 35 to 40 mm long at the completion of metamorphosis. The sardine does not have as marked a metamorphic stage as many other isospondylid fishes, including the anchovy.

Most clupeid larvae are remarkably similar in appearance and even in basic pigmentation. If larvae of the Pacific and the European sardine were mixed together in a sample, for example, it is doubtful whether the two species could be separated.

The sequence in which fins form in sardine larvae is as follows : larval pectoral (without rays), dorsal, caudal, anal, pelvic and pectoral with rays. The dorsal and anal fins lay down all but the anterior one or two rays before pelvic and pectoral ray formation is initiated. Although principal caudal rays are formed by the time the caudal fin becomes terminal (at about 14 mm), procurrent ray formation is not completed until near the close of metamorphosis.

The predorsal distance is greater in larval sardines than in juveniles. At the beginning of metamorphosis the origin of the dorsal is opposite the centrum of the 28th vertebra, by the end of metamorphosis it is opposite the 18th vertebral centrum. The prepelvic distance, on the other hand, is less in larvae than in juveniles. The backward shift during metamorphosis is from approximately the 18th to the 22nd vertebral centra. At the beginning of metamorphosis the pelvic fins, consequently, are forward of the dorsal fin by the width of ten vertebral centra; at the conclusion of metamorphosis the insertion of the pelvic fin is considerably behind the origin of the dorsal fin. The anal also moves somewhat forward during metamorphosis; the origin shifts from opposite the 41st vertebral centrum to opposite the 38th.

- Feeding

Arthur (1956) has done the most complete analysis of the feeding of larval Sardinops caerulea. He found that the identifiable food of sardine larvae consisted almost entirely of eggs, nauplii and juvenile stages of copepods. The percentage composition of food objects found in the digestive tract of sardine larvae of three size groups is summarized in Table VI.

Table VI

FOOD OF SARDINE LARVAE

Food item	Larvae to 5.5 mm Percentage of total	Larvae 6.0-9.5 mm Percentage of total	Larvae 10.0-25.0 mm Percentage of total
Copepod eggs	22.0	10.8	28.6
Copepod nauplii	54.5	76.3	37.1
Copepodid stages	0.3	3.4	31.4
Miscellaneous	4.4	-	-
Unidentified material	18.8	9.5	2.9
Total	100.0	100.0	100.0

Food items that could be utilized by sardine larvae just beginning to feed (4.0-4.5 mm larvae) were found to be limited to objects between approximately 0.02 to 0.08 mm in greatest width or depth. Larvae of about 10 mm in length were able to utilize items up to 0.20 mm.

Since gill rakers do not develop until metamorphosis, sardine larvae do not obtain food by filtering but by selective, particulate feeding. Vision is necessary for feeding, hence the incidence of feeding at night is low.

- Rates of: development and survival

Only rough estimates have been obtained of the growth rate of sardine larvae. It is estimated that a sardine larva requires between one and two months to complete the planktonic phase of its life history. The midpoint of this estimate, 45 days, is taken as an approximation of the average age of a sardine larva 24 mm in length. It is assumed that growth of larvae can be represented by a simple logarithmic curve (Ahlstrom, 1954). More adequate growth data are badly needed.

Growth during the early larval period, through the completion of yolksac absorption, has been fairly well defined (Farris, 1959). Growth as measured by increase in length is at a much faster rate during the first day after hatching than subsequently.

The estimated survival per 100,000 eggs (1951 year class) was one per cent for 12 mm larvae, 0.1 per cent for 21 mm larvae (Ahlstrom, 1954).

- Parasites and predators

No parasites have been observed on the thousands of sardine larvae that have been identified and measured during the CCOFI surveys.

Predators : filter-feeding nekton, including fish and crustacea; numerous organisms in the plankton including chaetognaths, Candacia (copepods), siphonophores, jellyfish, ctenophores and fish larvae.

3.3 Adult history

3.3 1 Longevity

Sardines of 13+ years have been recorded from several Pacific coast ports by Mosher and Eckles (1954). Most year classes of sardines have been reduced to approximately one per cent of their strength at recruitment to the fishery, by the time they reach five or six (occasionally seven) years of age (see section 4.1.2).

3.3.2 Hardiness

The Pacific sardine is a temperate water species. Although the temperature range over which it can live has not been critically delimited, it is approximately between 7°C and 28°C. Sardine spawning seldom occurs at temperatures below 13°C or above 22°C.

The Pacific sardine is only moderately hardy. It is difficult to maintain in aquaria. However, it survives well enough in bait wells of tuna clippers to be carried long distances - such as between California and the Galapagos Islands.

3.3.3 Competitors

The sardine's principal competitor for food is the northern anchovy. Competition begins in the larval stage and continues through life. The areas of distribution of the two species are similar, both occurring in greatest abundance between Point Conception, California and Magdalena Bay, southern Baja California. Adult sardines are often taken in "mixed" schools, occurring with jack mackerel or Pacific mackerel. It is doubtful whether either species is as directly a competitor of the sardine as the northern anchovy.

3.3.4 Predators

Studies on the food habits of predaceous fishes that inhabit the same water as the Pacific sardine are too limited to give a satisfactory evaluation of their importance as predators on the sardine. Predaceous fishes would include tunas, sharks, yellowtail, barracuda, bonito, marlin, hake, Synodus and mackerel. Other important predators are sea lions, porpoises, whales, and birds, especially sea gulls, pelicans, and cormorants.

3.3.5 Parasites and diseases

A limited study of parasites of Sardinops caerulea is being made in connection with studies on subpopulations.

Three internal parasites have been found in sardines which have some promise as "natural tags". Myosaccium ecaude (Montgomery), a digenetic trematode and Contracaecum sp., an intestinal nematode, are fairly abundant and show interesting differences in incidence of infection. Contracaecum tends to occur in more sardines at the southern part of the range (off central Baja California) than in the northern part, while Myosaccium occurs less frequently in the south as compared to the north. A third parasite, another nematode belonging to the superfamily Ascaroidea, is less common than the other two species, and so far has been taken most frequently in the southern part of the range. A few other parasites have been taken in the sardine, non in any abundance.

3.4 Nutrition and growth

3.4.2 Food (type, volume)

The sardine is a filter-feeding fish that appears to do a certain amount of selective feeding. The close correlation found by Hand and Berner (1959) between stomach contents of adult sardines and plankton collected at the same time, led them to conclude that the sardine is an omnivorous filter feeder. Radovich (1952) presented evidence that particulate feeding may be important at times, since he found sardines gorged with one-and-a-half inch long postlarval anchovies.

Most investigations have found that crustaceans, especially copepods, are the major food item in sardine stomachs, but a wide variety of other zooplankton organisms also occur in lesser quantities. The importance of diatoms and dinoflagellates in the diet appears to vary with region. For example, Hart and Wailes (1931) found a high proportion of diatoms in the stomach contents of sardines collected in British Columbian waters in 1929. The other workers noted above found that, in quantity, diatoms and dinoflagellates constituted only a minor item in the stomach contents of sardines collected off southern California and Baja California.

Hand and Berner note that sardines stop feeding when in a spawning condition. The samples on which they based these observations were taken off central Baja California in September, 1952.

3.4.3 Relative and absolute growth patterns and rates

Phillips (1948) and Felin (1954) have dealt with growth of sardines collected in different areas. One-year-old sardines caught off southern California were observed to be slightly larger than one-year-old fish taken off central California or British Columbia. After the one-ring stage, there is a deceleration of growth in sardines from southern California as compared to fishing areas to the north. Sardines of three rings or older are considerably larger, on the average, in catches from British Columbia than fish of these ages taken off San Pedro, while sardines taken off central California are intermediate in size. The average size of fish of ages one to seven in the catches from four fishing areas are summarized in Table VII. Ten year classes are used in obtaining the average for each area. Sardines in each of the four areas have a different growth pattern, most markedly different between San Pedro and British Columbia.

In older sardines there is a definite north-south cline in size of fish of the same age. The increased size of northern fish may be due either to the larger fish of a year class performing the longer migrations northward, or to better growth in northern latitudes associated with more abundant food.

Table VII

DIFFERENCE IN SIZE AT SAME AGE OF SARDINES
IN THE COMMERCIAL CATCHES OF FOUR FISHING AREAS

Age	San Pedro	Monterey	San Francisco	British Columbia
	LS (millimetres)			
1-ring	183	172	176	179
2-ring	200	203	207	201
3-ring	208	218	221	223
4-ring	214	225	227	236
5-ring	220	232	232	242
6-ring	226	240	240	246
7-ring	-	243	247	249

3.5 Behaviour

3.5.1 Migration and local movements

Tagging experiments conducted between 1935 and 1942 by California, Oregon, and British Columbia fisheries research groups gave direct information about movements of sardines. Over 140,000 fish were tagged and released in four general areas : Pacific Northwest, central California, southern California, and Baja California. The research showed the following :

(a) Fish tagged at any locality from southern California north were recovered on all fishing grounds from southern California to British Columbia. Fish tagged off Baja California were recovered in large numbers in the southern California catch, moderately in the central California catch and negligibly in the catch of the Pacific Northwest.

The recoveries per 1,000 fish tagged from each of the four major release areas are shown in Table VIII.

(b) Fish tagged and released from the southern California area approached a random dispersal throughout the fishing areas. Tagged fish released off central California were recovered mostly off central California or the Pacific Northwest, and only in lesser numbers off southern California.

(c) Older fish tended to accumulate at the northern end of the range, becoming increasingly available to the fishery in the Northwest after tags had been out for three or more seasons.

The tagging experiments furnished incontrovertible evidence of extensive movements of sardines between the fishing ports. Northward movements took place during the summer, southward in late fall and winter.

Table VIII

SARDINE TAG RECOVERIES (AT 100 PER CENT EFFICIENCY) PER 1,000 FISH TAGGED

Recovery area	Release area			
	Pacific Northwest	Central California	Southern California	Baja California
Pacific Northwest	2.1	6.2	7.2	0.1
Central California	2.4	59.5	53.7	12.2
Southern California	1.5	14.1	29.4	44.1
Baja California	No recovery facilities			
Total	6.0	79.8	90.3	56.4

Local movements within a fishing area are being investigated for the years since 1946-47. Daily catch locations for 1950-51, a good season in southern California, have been analyzed in terms of coastwise movements. The October catches were drawn from seven northward progressions, each closely succeeding the other. In November there was still some evidence of northward progression, but the major portion of the catch suggested southward movement, as did the entire catch in December.

3.5.2 Schooling
3.5.3 Reproductive habits

Sardines fished by the commercial fleet occur in schools of various sizes - from a few tons to several hundred tons. The depth to which schools may descend is not known. They are fished at or near the surface.

Young sardines apparently do not occur in the large dense schools so characteristic of adult fish. Immature fish are seldom caught by the purse seine fishermen who depend upon sight and echosounding equipment to locate fish. Apparently schooling behaviour is related to maturity. Even two-year-old fish are only partially available.

Sardines are seldom observed during the spawning period, and as a result the size of aggregations during this period is imperfectly known. Schools that have been observed during this period have been small, compact masses of fish swimming rapidly about.

4 POPULATION (STOCK)

4.1 Structure

4.1.1 Sex ratio

Male and female have approximately a 1 : 1 ratio in the commercial sardine catch. The percentage of females in the samples used for age determinations during a 15-year period (1941-42 through 1955-56 seasons) was 49.4 per cent. The season of the series with the lowest percentage of females in the catch was 1955-56 with 46.2 per cent; the season with the highest percentage was 1951-52, with 53.8 per cent.

4.1.2 Age composition
4.1.3 Size composition

Length frequency data have been taken systematically on landings of the Pacific sardine since November 1919, hence are available for a period of 40 years. Technical problems delayed the aging of sardine landings, but these were solved by Walford and Mosher (1943a and b). These workers commenced with young sardines and later included older fish. Both scales and otoliths were found to be equally useful in determining age. Because of the simplicity in handling scale samples, particularly after a simple method was developed of mounting scales dry and projecting their enlarged image, this method of age determination was adopted. A cooperative program of age determination has been carried on since the 1941-42 season.

Prior to this, a number of important papers had dealt with various aspects of the age composition of the landings in California and British Columbia (Andrews, 1928; Clark, 1931, 1936, 1939; Hart, 1933; Higgins, 1926; Phillips, 1937; Scofield, 1926; Sette, 1928; Thompson, 1926).

During the early years of the fishery, the size of sardines in the catch changed from one level during the fall fishery to a larger size level in the winter fishery. The fall fishery occurred during August through November in Monterey and San Francisco, the winter fishery during December and January. October to December comprised the fall fishery in southern California, January to March the winter fishery. An indirect method of assessing age by tracing dominant size groups through the fishery was developed during this period.

The age composition of the commercial catch of sardines has been determined annually since the 1941-42 season. The first paper in the series (Felin and Phillips, 1948) dealt with the age and length composition of the catch at all Pacific coast ports for six seasons, 1941-42 through 1946-47. Since then, the data have been published annually (see Wolf et al., 1958, for bibliography). The age composition of commercial landings, beginning with the 1941-42 season, is summarized in Table IX.

Mosher and Eckles (1954), utilizing otolith samples collected during the 1932-33 through 1937-38 seasons, were able to supply age determinations for these years, especially for the ports of Monterey and San Pedro. More recently, Wolf (in press), utilizing scale samples and length frequency data, has supplied some age data for the intervening years (1938-39 through 1940-41). Age determinations for these earlier years are approximations only, as collections of otoliths and scales were made only sporadically.

Table IX

AGE COMPOSITION OF PACIFIC SARDINE CATCH 1941-42 THROUGH 1957-58 SEASONS

Year	Tons	Number	Number of individuals in millions at age								
			0	1	2	3	4	5	6	7	8 and older
1941-42	679,460	6040.6	-	466.3	3,196.3	1,659.3	444.7	184.2	48.1	24.0	17.7
1942-43	570,210	4343.4	-	284.8	1,077.4	1,905.7	764.6	210.5	80.0	14.8	5.6
1943-44	570,910	3966.0	-	476.6	596.7	1,031.0	1,228.5	425.3	148.3	44.4	15.2
1944-45	604,480	4076.0	-	431.1	1,261.0	757.3	641.6	654.8	237.6	73.0	19.6
1945-46	435,420	2963.3	-	247.9	923.6	857.6	482.3	233.5	145.2	54.2	19.0
1946-47	242,050	1917.5	3.1	762.1	520.2	369.0	142.2	56.2	34.9	23.4	6.4
1947-48	118,900	964.6	28.4	259.2	314.2	171.9	96.0	55.2	17.6	11.9	10.2
1948-49	165,140	1522.3	0.7	499.9	759.4	164.2	59.5	21.2	7.3	3.3	6.8
1949-50	334,120	2754.2	-	215.5	1,416.2	768.5	225.8	111.1	12.9	1.1	3.1
1950-51	350,550	2589.8	-	-	1,121.4	989.8	388.4	74.0	15.7	0.4	0.1
1951-52	136,010	1041.6	-	12.3	60.1	713.3	176.8	61.6	14.6	2.6	0.3
1952-53	11,220	77.2	-	0.7	3.8	17.1	42.0	10.4	2.9	0.3	-
1953-54	10,020	61.9	-	1.5	3.4	20.4	6.8	26.3	2.8	0.6	0.1
1954-55	75.960	592.9	3.8	2.8	193.3	217.5	68.0	41.1	60.8	5.6	-
1955-56	74,960	527.0	-	11.0	68.9	257.6	134.6	24.3	10.1	19.6	0.9
1956-57	38,620	224.4	-	-	16.9	76.3	96.6	23.3	2.9	0.9	7.5
1957-58	23,620	183.0	2.6	19.5	41.1	56.4	28.4	28.1	5.5	0.8	0.6

4.2 Size and density

4.2.1 Average size

Measures of population size are difficult to obtain for pelagic marine fishes. Because of the uncertainties attendant upon such estimates, it is desirable to estimate population size by several independent methods. Four methods have been used in estimation of the population size of the Pacific sardine : catch data, tagging data, egg census (and fecundity), and scouting surveys. Estimates of the average population off California over the period 1936-37 to 1943-44 based on tagging data range from nine- to 16 billion fish, depending upon the method followed in combining data from southern and central California (Clark and Marr, 1955). The lower value is certainly too low, as the average population for the same period, based on accumulated age data, is eight billion fish. The accumulated age estimate for any given season is the number of fish actually caught in that season, plus the landings of the same year classes in subsequent seasons. It is minimal because it represents only the segment of the population that died as a result of being caught by fishermen.

Accumulated age estimates of population abundance from 1939-40 to 1952-53 are given in Table X. The sardine population as at its highest level in the 1941-42 season (11.5 billion fish); at its lowest in the 1952-53 season. (This latter estimate reflects, in part, lowered availability of sardines to the fishery).

Estimates of population size derived from egg census data (fecundity assumed to constant at 100,000 eggs per female) lie between 2.3 billion (1957) and 12 billion fish (1951).

Table X

ACCUMULATED AGE (VIRTUAL POPULATION) ESTIMATES OF POPULATION ABUNDANCE (in billions of fish)

Season	Estimated abundance	Season	Estimated abundance
1939-40	6.8	1946-47	1.7
1940-41	8.4	1947-48	1.4
1941-42	11.6	1948-49	2.7
1942-43	9.1	1949-50	4.3
1943-44	7.0	1950-51	3.7
1944-45	5.8	1951-52	1.2
1945-46	3.6	1952-53	0.4

4.2.4 Changes in density

Changes in density are best shown by the return per unit of effort to the fishermen. Boat catch data are given by Marr (1950) for the sardine fishery off Oregon and Washington. The returns per unit of effort to California fishermen are discussed by Clark (1939), Silliman and Clark (1945), Clark and Daugherty (1950 and 1952), and Clark (1956).

For California, the average lunar month catch per boat (the standard adopted by Clark in her latter papers) increased from 1932-33 to 1934-35, decreased to 1937-38, increased somewhat until 1942-43. Then began a slight decline which accelerated after 1944-45 and continued through 1947-48. A slight upward trend occurred in the 1948-49 and 1949-50 seasons, followed by a decline in 1950-51 and 1951-52 and a precipitous dip in 1952-53, with only a partial recover since then.

4.3 Natality and recruitment

The strength of year classes in the Pacific sardine fishery between 1939 and 1953 are given in Table XI. These estimates are based on the contribution of each year class to the fishery throughout its life. Estimates of the 1951 through 1953 classes are incomplete, since they may still contribute to the commercial catch.

Table XI

ESTIMATES OF YEAR CLASS STRENGTH, BASED ON THEIR CONTRIBUTION TO THE COMMERCIAL CATCH (in billions of fish)

Year class	Estimated abundance	Year class	Estimated abundance
1939	7.16 [2/]	1947	3.13
1940	3.50	1948	2.21
1941	2.20	1949	0.14
1942	2.80	1950	0.13
1943	1.85	1951	0.39 (inc.)
1944	1.13	1952	0.58 (inc.)
1945	1.56	1953	0.18 (inc.)
1946	2.24		

2/ Exclusive of fish taken as 0 and one-year-olds.

The largest year class in the series, 1939, contributed over seven billion fish at ages two and older. More than three billion fish were landed from both the 1940 and 1947 classes. Beginning with the 1949 season, year classes have been exceptionally poor. The best of this group, the 1952 class, has furnished less than 0.6 billion fish.

There are exceedingly large differences in the strength of individual year classes. The 1939 class has supplied over 50 times as many fish to the commercial catch as either the 1949 or 1950 classes.

The nine classes that followed 1939 (1940-48) were fairly uniform in size, the largest contributing only three times as many fish as the smallest. Thereafter, the year class strength dropped to a level that has been only one-tenth as large, on the average, as that during the preceding decade.

Estimates of year class size based on their numbers in the commercial catch are minimal. Most year classes are not completely recruited until age three. Members of a year class that die from causes other than fishing mortality are excluded from the estimates. Estimates are influenced by availability. The low estimates of the 1949 class and subsequent ones are undoubtedly due, in part, to their low availability to the commercial fishery.

4.4 Mortality, morbidity

The most comprehensive table dealing with estimates of mortality rate is contained in Clark and Marr (1955). It is reproduced here, as Table XII.

4.5 Dynamics of population

Has been developed in other sections, hence not separately treated.

4.6 Relation of population to community and ecosystem, biological production, etc.

The region in which the Pacific sardine is now found can be divided into five roughly defined areas : north of Point Conception, southern California, northern Baja California, central Baja California, and the Gulf of California.

The northern region is characterized by high plankton volumes containing a large proportion of crustacean plankton (copepods and euphausiids). The southern California area is a variable region both from the standpoint of plankton volume and composition, depending in part on the extent of upwelling and on incursion of waters from the west and south. In the area of northern Baja California, plankton volumes are usually low except for a band near shore. The incursion of plankton from oceanic waters from the central Pacific is particularly felt in this area. Central Baja California is another variable region where plankton production is strongly influenced by upwelling or its absence, particularly south of Point San Eugenio. The Sebastian Viscaino Bay region is an area of high productivity. A second but less common influence in this area is the incursion of tropical water from the south. Although some sardines occur off southern Baja California, particularly in the bays, it is not an important area for sardines, probably because it is a border area between California Current waters and southern tropical waters.

Table XII

PACIFIC SARDINE : ESTIMATES OF MORTALITY RATES (percentage)
(Clark and Marr, 1955)

Season	Total mortality				Fishing mortality						Natural mortality		
	1	2	3	4	5	6	7	8	9	10	11	12	13
	Catch, effort and age data		Tagging	Accumulated age	Catch, effort and age data		Tagging		Scouting	Egg censuses	Tagging		Scouting
	No. 1	No. 2			No. 1	No. 2	No. 1	No. 2			No. 1	No. 2	
1932-33	51	39	-	24	22	8	a	a	-	-	-	-	-
1933-34	55	42	-	25	28	12	v	v	-	-	-	-	-
1934-35	59	51	-	33	32	23	e	e	-	-	-	-	-
1935-36	63	50	-	36	37	21	r	r	-	-	-	-	-
1936-37	71	71	-	59	48	48	28-50 a	22-39 a	-	-	33	39	-
1937-38	72	55	65	53	50	27	28-50 g	22-39 g	-	-	33	39	-
1938-39	75	-	66	59	53	-	28-50 e	22-39 e	-	-	33	39	-
1939-40	73	-	75	50	51	-	28-50	22-39	-	-	33	39	-
1940-41	69	-	50	45	46	-	28-50 o	22-39 o	-	-	33	39	-
1941-42	74	59	48	49	52	32	28-50 v	22-39 v	-	-	33	39	-
1942-43	69	62	58	45	45	36	28-50 e	22-39 e	-	-	33	39	-
1943-44	71	67	87	50	48	44	28-50 r	22-39 r	-	-	33	39	-
1944-45	73	73	77	62	51	52	-	-	-	-	-	-	-
1945-46	73	69	70	75	50	46	- p	- p	-	-	-	-	-
1946-47	81	45	-	71	61	16	- e	- e	-	-	-	-	-
1947-48	81	41	-	50	61	10	- r	- r	-	-	-	-	-
1948-49	68	38	-	37	44	6	- i	- i	-	-	-	-	-
1949-50	66	49	-	58	41	20	- o	- o	-	-	-	-	-
1950-51	85	51	-	74	68	24	d	d	21	46	-	-	40
1951-52	-	-	-	90	-	-	-	-	-	7	-	-	-
1952-53	-	-	-	80	-	-	-	-	-	3	-	-	-
1953-54	-	-	-	-	-	-	-	-	-	-	-	-	-

1 Pertinent to the available population only, with natural mortality constant at about 33 per cent.
2 Pertinent to more nearly the total population, with natural mortality constant at about 33 per cent.
3 From tag recovery tables given by Clark and Janssen (1945).
4 Numbers of fish caught divided by "accumulated age" estimate of number of fish in the population.
5 See footnote 1.
6 See footnote 2.
7, 8 Higher values from tagging data given by Clark and Janssen (1945); lower values derived by Marr from the same data.
9 Derived from data given by Radovich (1952).
10 Numbers of fish caught divided by "egg censuses" estimates of a number of fish in the population.
11 See footnote 3.
12 See footnote 8.
13 See footnote 9.

5 EXPLOITATION

5.1 Fishing equipment

5.1.1 Fishing gear

Sardines are taken almost entirely in round haul nets, either a purse seine or a ringnet. The length of the fishing vessel varies from about 40 to 110 ft. The length and depth of nets are roughly proportional to vessel size.

There have been a number of improvements in gear and fishing aids during the past 25 years. A few of the more important are listed here :

(a) radios (ship to ship) - first used in California about 1933; all vessels were equipped with transmitting and receiving sets by 1940;

(b) echosounding gear - first used in 1944; now installed on all sardine fishing vessels;

(c) motor skiffs - first used in 1944; the majority of the larger boats now have them;

(d) synthetic netting materials, especially marlon and nylon, were used in combination with other netting materials until recently; now some vessels employ nets made entirely of nylon;

(e) airplane scouting - daytime airplane scouting used for locating sardines in the Pacific Northwest in the early 1940's; employed off southern California for anchovies, mackerel, and tuna fishing as early as 1950; night plane scouting for sardines began in 1954;

(f) power block - recently introduced on larger purse seine vessels, especially for use in tuna purse seining, but also available for sardine fishing.

5.1.2 Fishing boats

With the decrease in the sardine catch which began in the 1945-46 season off central California, and which extended to all fishing areas after the 1951-52 season, there has been a decrease in the purse seine fleet. There has been no addition to the fleet of larger purse seine vessels (the vessels over 60 ft in length) since 1948. Some vessels have been diverted to other fisheries, particularly tuna; some vessels have been sold out of the state or country, many to Mexico; others have been wrecked. The fleet of large purse seine vessels was at an all-time peak of about 300 boats in the mid- and late 1930's, and decreased to about 200 in the early1940's when some vessels were diverted to war use. The fleet increased in size after World War II through conversion and new building, to approximately 230-240 vessels. During the past two seasons (1957-58 and 1958-59), there have been approximately 80 larger vessels.

Small vessels employing purse seine or lampara nets have varied in number from year to year, since they engage in other fisheries besides sardine. They enter or leave the sardine fishery as prices and availability vary. The number of these remains fairly high, and was about 70 in the 1958-59 season.

The highest total fleet counts have been 379 in the 1937-38 season, and 372 in the 1949-50 season. The fleet in the latter season included 135 smaller vessels.

5.2 Fishing areas

5.2.1 General geographic distribution

Historically, there are eight important fishing areas, listed from north to south :

(1) British Columbia;

(2) Washington - landings in the Gray's Harbor area;

(3) Oregon - Astoria, earlier Coos Bay;

(4) San Francisco, California, including Richmond, Benicia, Martinez and Pittsburg;

(5) Monterey, California, including Moss Landing;

(6) San Pedro, California, including Wilmington and Long Beach;

(7) San Diego, California;

(8) Enseñada, Baja California, Mexico.

Catch statistics, by area, listed in section 5.4, show the sequence of development and decline of the fishing in each area.

During the past decade, the fishing has been non-existent in the Pacific Northwest, sporadic and low in level off central California, exeedingly variable off southern California, since both the highest and lowest catches on record occurred within a space of three years (1950-51 to 1953-54).

5.3 Fishing seasons

5.3.3 Dates of beginning, peak, and end of season

The California fishery has been the principal one for sardines. Fishing has been limited to definite seasons, which differed in the central and southern fishing areas. The seasons are shown below :

Central California (Monterey and San Francisco)

1929-47	1 August - 15 February
1948-56	1 August - 15 January
1957 to date	1 August - 31 December

Southern California (San Pedro)

1929-43	1 November - 31 March
1944-47	1 October - 1 March
1948-56	1 October - 1 February
1957 to date	1 September - 31 December.

There has been no seasonal restriction on catch in either the Pacific Northwest or Baja California.

Although fishing seasons in California are set by law, they were originally requested by the industry. The fishing seasons were set to cover the period of high availability and good yield in each area.

In recent years, fish have been most available during the early part of the season, and have become scarce during the latter part of the fishing season. The 1958-59 season was an exception; sardines were available for the entire season. Unusually warm water conditions prevailed during this season.

An historical account of differences in catch within and between seasons and ports will not be attempted, as it would require a lengthy exposition. Interesting facets of this problem are discussed for the 1932-33 through 1941-42 seasons by Silliman and Clark (1945).

5.4 Fishing operations and results

5.4.3 Catches

The landings of sardines from eight important fishing areas are shown in Table XIII. The catch of floating plants which operated beyond territorial waters off San Francisco between 1930 and 1938 is listed separately. The landings at Ensenada, reported from the 1951-52 season to date, include only the landings from the months which correspond to the southern California fishery.

There has been a marked decline in the Pacific sardine fishery, commencing with the 1945-46 season. The decline was first evidenced in the Pacific Northwest, and moved progressively southward. The fishery at San Pedro held up through the 1951-52 season. The exceedingly low catches in the 1952-53 and 1953-54 seasons were due in part to lowered availability, in part to the recruitment to the fishery or the two poorest year classes on record (1949 and 1950). The 1958-59 catch, the largest since the 1951-52 season, had unusually high availability of sardines off California, associated with warmer than average water conditions. The influence of availability of sardines on the catch has been strongly felt during the past decade.

A brief discussion of fishing success (return per unit of effort) is presented in section 4.2.

5.5 Fisheries management and regulations

Fishing seasons in California were listed in section 5.3.3 Other regulations in California include :

(a) Reduction permits : Reduction of whole fish to fishmeal and oil has been allowed in California only under permit. The initial issuance of permits was more or less forced on the California Fish and Game Commission to counteract the activity of floating reduction ships operated outside the territorial waters of California (1926-38). The tonnage allowed on each permit varied from a high of 12,000 tons in 1934-35 to a low of less than 1,000 tons in 1948-49. In 1949, as a result of concern over sardine scarcity, the Fish and Game Commission adopted a policy of denying all sardine reduction permits, and has continued this ever since. At present prices paid for sardines (US $50 per ton) and the depressed market for fish oil and meal, it would be uneconomical to reduce sardines, even if reduction were permitted.

Table XIII

CATCH OF PACIFIC SARDINE, 1916-17 THROUGH 1957-58 (in tons)

Season	British Columbia	Washington	Oregon	California					Ensenada	Grand total
				Floating Plants	San Francisco	Monterey	San Pedro	San Diego		
1916-17 3/	-	-	-	-	-	7,710	17,380	2,440	-	27,530
1917-18	80	-	-	-	70	23,810	41,340	7,360	-	72,660
1918-19	3,640	-	-	-	450	35,750	32,530	6,810	-	79,180
1919-20	3,280	-	-	-	1,000	43,040	16,580	6,410	-	70,310
1920-21	4,400	-	-	-	230	24,960	11,740	1,520	-	42,850
1921-22	990	-	-	-	80	16,290	19,220	910	-	37,490
1922-23	1,020	-	-	-	110	29,210	33,170	2,620	-	66,130
1923-24	970	-	-	-	190	45,920	35,040	2,780	-	84,900
1924-25	1,370	-	-	-	560	67,310	96,330	8,820	-	174,390
1925-26	15,950	-	-	-	560	69,010	61,990	5,710	-	153,220
1926-27	48,500	-	-	-	3,520	81,860	64,720	2,110	-	200,710
1927-28	68,430	-	-	-	16,690	98,020	67,900	4,650	-	255,690
1928-29	80,510	-	-	-	13,520	120,290	119,250	1,420	-	334,990
1929-30	86,340	-	-	-	21,960	160,050	140,540	2,620	-	411,510
1930-31	75,070	-	-	10,960	25,970	109,620	38,490	80	-	260,190
1931-32	73,600	-	-	31,040	21,610	69,080	42,660	260	-	238,250
1932-33	44,350	-	-	58,790	18,630	89,600	83,600	60	-	295,030
1933-34	4,050	-	-	67,820	36,340	152,480	125,050	1,750	-	387,490
1934-35	43,000	-	-	116,480	69,000	230,860	178,820	4,860	-	643,020
1935-36	45,320	10	26,230	150,830	76,150	184,470	138,400	10,650	-	632,060
1936-37	44,450	6,560	14,200	235,590	141,100	206,710	138,110	4,590	-	791,310
1937-38	48,080	17,100	16,660	67,550	133,720	104,930	109,950	380	-	498,370
1938-39	51,770	26,480	17,020	43,890	201,200	180,990	146,400	2,780	-	670,530
1939-40	5,520	17,760	22,330	-	212,450	227,870	101,820	110	-	587,860
1940-41	28,770	810	3,160	-	118,090	165,700	175,590	1,200	-	493,320
1941-42	60,050	17,100	15,850	-	186,590	250,290	148,910	1,580	-	680,370
1942-43	65,880	580	1,950	-	115,880	184,400	201,510	2,870	-	573,070
1943-44	88,740	10,440	1,820	-	126,510	213,620	135,310	2,690	-	579,130
1944-45	59,120	20	-	-	136,600	237,250	178,290	2,770	-	614,050
1945-46	34,300	2,310	90	-	84,100	145,520	173,110	950	-	440,380
1946-47	3,990	6,140	3,960	-	2,850	24,900	195,500	4,770	-	242,110
1947-48	490	1,360	6,930	-	380	11,640	95,710	2,430	-	118,940
1948-49	-	-	5,500	-	1,370	34,710	120,630	2,940	-	165,150
1949-50	-	-	-	-	17,535	128,410	184,960	3,210	-	334,115
1950-51	-	-	-	-	12,730	32,080	302,810	2,930	-	350,550
1951-52	-	-	-	-	-	15,730	110,070	1,340	8,870	136,010
1952-53	-	-	-	-	-	44	4,450	30	6,700	11,224
1953-54	-	-	-	-	-	-	2,860	320	6,850	10,030
1954-55	-	-	-	-	-	830	65,920	510	8,710	75,970
1955-56	-	-	-	-	-	-	73,260	-	1,710	74,970
1956-57	-	-	-	-	-	60	32,590	-	5,970	38,620
1957-58	-	-	-	-	-	-	21,110	-	2,510	23,620
1958-59	-	-	-	-	-	24,614	78,007	-	7,793	110,414

3/ Data for 1916-17 through 1945-46 seasons from Clark, 1948. Remainder from Wolf (in press).

(b) Canning : the present case pack requirements in California have been in effect since 1929. Canners are required to pack at least 13.5 cases per ton of fish received. A standard case contains 48 one-pound oval cans of sardines, or equivalent. In recent years, the case pack has averaged between 20 and 22.5 cases per ton.

(c) Closed areas : some areas off southern California are closed to sardine fishing. These include Santa Monica Bay, waters around Catalina Island, and several areas in Orange County.

(d) Size limits : seldom imposed. In December 1947, a seven-inch limit was placed on sardines, with a 25 per cent load tolerance. It was continued during the 1948-49 season at a revised eight-inch limit with similar load tolerance.

(e) Load limits : not imposed by law, often employed by agreement between canners and fishermen.

6 ACKNOWLEDGMENTS

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EXTRAIT
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No. 12.

Plankton Volume Loss with Time of Preservation[1])

By

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Abstract

Because of the difficulty of duplicating preserved plankton volume measurements after the samples have stood for a period of time, an investigation was made on the time changes that occur in preserved plankton volumes with differing compositions.

Volume measurements were made over a two-year period on 12 selected samples of zooplankton. The samples showed losses of from 15% to 87% of their volume at collection. The most marked changes in volume occurred at preservation and during the first day thereafter. Some samples showed little or no subsequent decrease in volume over a two-year period, others showed a continuing but decelerating decrease with time. The amount of decrease is related to constituents, being least for samples in which crustaceans made up most of the volume, greatest for samples in which salps were dominant.

Constituent composition (volumes occupied by the major constituent groups) will change relative to each other with changes in sample volume. Hence it is important to make constituent determinations either at the time of collection, before preservation, or after volumes have reached comparative stability (1 to 2 years after preservation).

"Wet" plankton volume determinations (sometimes called "displacement" volumes) were used during the study. Estimation of the amount of interstitial liquid retained by test samples (determined by a colorimetric technique ranged from 17% to 45% of the total "wet" volumes with most determinations being between 31% and 40%).

Dry weight determinations of the 12 test samples gave volumes of from 56 mg to 116 mg per gramme of preserved plankton (without interstitial liquid) with most values clustered between 80 mg and 100 mg despite differing composition of samples. The large water adjustments that take place in salps and siphonophores during preservation concentrate the organic constituents in them relative to organisms possessing an exoskeleton (crustaceans, pteropods). Hence determinations made at equilibrium volumes (1 to 2 years after preservation) may be adequate measures of the "food value" of larger zooplankton organism (i.e. those retained by standard plankton nets).

Ash weight determinations were 6% to 18% of the dry weight. These values are too low to account for salts present in zooplankton constituents at time of collection (zooplankton organisms are usually isotonic with sea water), hence leaching of salts from the bodies of preserved organisms occurs at the time of volume adjustments.

[1]) U.S. Dept. Int. Fish and Wildl. Serv., Fish. Bull.

BANDJUNO A.S. Kbh.

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CONTRIBUTION

No. 157

alveston Biological Laboratory
. Bureau of Commercial F eries

Photoautotrophy in Gymnodinium breve Davis

Abstract. Pure cultures of the Florida "red-tide" flagellate required light and carbon dioxide for growth. Multiplication in darkness was not supported by any of a number of organic compounds and mixtures. The ecological importance of micronutrients is suggested.

The catastrophic mortalities of marine animals associated with dense populations of the dinoflagellate, *Gymnodinium breve* Davis, have occasioned considerable interest in the biological requirements of this organism (*1*). Several environmental factors have been suggested as agents contributing to "red-tide" outbreaks which recur along the Florida Gulf coast. Such phenomena have been more closely associated with extended periods of heavy rain than with any other condition (*2*). In view of the prevalence of organic soils in this locality (*3*), and the fact that aqueous extracts of organic soil promoted growth in the first successful cultures of *G. breve*, it seemed that river discharge, representing soil drainage, might be "instrumental in initiating" blooms of this organism (*4*). Wilson and Collier also suggest that decaying red-tide-killed fish "imparted nutrients that helped to perpetuate the bloom" (*4*). In the light of references to the widespread occurrence of heterotrophy among dinoflagellates (*5*), it seemed appropriate to determine whether the organic content of Florida river waters or coastal fishes might provide a direct source of energy for multiplication in *G. breve*. Accordingly, my report represents an attempt to define the heterotrophic capacities of this organism.

Axenic, 10-ml cultures of the flagellate were prepared in screw-capped tubes, using about 200 motile cells for inoculum, and a virtually inorganic, artificial sea water medium (*6*). Since the basic medium permits neither multiplication nor survival of *G. breve* in darkness, it was assumed that the degree to which added substances could serve as energy sources would be related to their abilities to support multiplication in the dark. The extreme sensitivity of this organism renders the incidence and rate of multiplication somewhat unpredictable, even in replicate cultures. This type of variation in results was avoided by starting all cultures with the basic medium only and illuminating them (500 ft-ca) until successes and failures were obvious at 10 × magnification. Cultures showing comparable growth (at least a tenfold population increase within 4 weeks) were then selected for use in this work. Aseptic additions of the organic compounds were made to all except control tubes, and the cultures were placed in darkness. An identical series of enriched and unenriched cultures was illuminated as above. All cultures were maintained at 25° ± 1°C. Estimates of population growth and survival were made microscopically.

One of the Florida soil extracts tested (prepared as described in (*4*) from soil obtained in the Fort Myers area) had also been used in natural Florida sea water media, in which it aided multiplication of *G. breve* in illuminated cultures. Each soil extract was tested at concentrations of 10 and 100 ml/liter. The fish extracts represented a filtered, 10-percent composite homogenate of muscle tissue from anchovy (*Anchoa mitchilli*), sand seatrout (*Cynoscion arenarius*), spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogon undulatus*), and striped mullet (*Mugil cephalus*), all common inhabitants of Florida west coast waters. This type of extract (either fresh or aged 3 days with uninhibited bacterial growth) was tested at a concentration of 5 ml/liter. The other organic substances were tested at several concentrations (0.1, 1.0, and 10.0 mg/liter) chosen to include and exceed the usual range of carbohydrate and total tyrosine concentrations found in Florida coastal water (*7*).

None of the organic compounds or mixtures (Table 1) supported multiplication or permitted extended survival in darkness. The longest survival was in the valeric acid cultures, which showed a 90-percent population reduction in 2½ weeks. No population increase was observed, however, in six replicate newly inoculated cultures containing valeric acid. All other cultures, both control and enriched, lost at least 90 percent of their initial populations in 1 to 2 weeks. Most of the identically enriched illuminated cultures did not decrease in population size during the same period, thus indicating no inhibitory effect for most of the compounds tested. The four exceptions contained 10 mg of linoleic acid, sodium oleate, sodium stearate, or kinetin per liter. Attempts to facilitate gas exchange by using very loosely packed sterile cotton plugs in place of the regular screw caps failed to extend survival without light. Attenuation of light over a period of several days, when introducing experimental cultures to darkness, also failed

Table 1. Organic substances tested as potential energy sources for *Gymnodinium breve*.

Substance	Substance
Carbohydrates and related compounds	*Lipids (Contd.)*
Arabinose	Butyrate
Ribose	Valerate
Xylose	Palmitate
Galactose	Stearate
Glucose	Oleate
Mannose	Linoleate
Fructose	
Sorbose	*Nitrogen compounds*
Rhamnose	Urea
Cellobiose	Alanine
Lactose	Aspartate
Maltose	Glutamate
Melibiose	Serine
Sucrose	Asparagine
Trehalose	Creatine
Melezitose	Adenine
Raffinose	Gelatin
α-methyl glucoside	
Glycogen	*Growth factors*
Inulin	Ascorbic acid
Pectin	Dehydroascorbic acid
Soluble starch	Biotin
	Cobalamin
Alcohols	Thiamine
Ethanol	Kinetin
Butanol	
Dulcitol	*Miscellaneous compounds and mixtures*
Mannitol	Beef blood serum
Sorbitol	Casamino acids
Ethylene glycol	Casein hydrolyzate
Glycerol	Coconut milk
Glycolytic and citric acid cycle constituents	Egg yolk
Glucose-1-phosphate	Fish extract
Fructose-6-phosphate	Liver concentrate
Phosphoglycerate	Malt extract
ATP	Mangrove extract
Citrate	Milk
Pyruvate	Milk protein hydrozyate
Isocitrate	Oxalate
α-ketoglutarate	Peptone
Succinate	Peptone-iron
Fumarate	Thioglycollate
Malate	Tartrate
Oxaloacetate	Tryptone
Lactate	Florida soil extracts (Ft. Myers) (St. Petersburg)
Lipids	Texas soil extract (San Antonio)
Formate	Yeast extract
Acetate	
Propionate	

to alter these results. Furthermore, removal of CO_2 from the medium by suspending 0.2 ml of 10 percent KOH in the gas phase of established cultures and sealing the tubes with paraffin prevented multiplication or survival of *G. breve* in illuminated cultures. (Similarly sealed cultures with 0.2 ml of distilled water suspended in the gas phase showed no change in population.)

One must conclude that this dinoflagellate is primarily photoautotrophic, requiring light and CO_2 for growth and survival. The present findings parallel those of Barker and of Provasoli and co-workers, who did not find organic metabolic substrates capable of supporting growth of photosynthetic dinoflagellates in darkness (*9*). The growth-stimulating effects of thiamine, biotin, and cobalamin in illuminated cultures (*8*) represent the only known deviation from strict photoautotrophy in *G. breve*. Provasoli also noted the importance of B vitamins to the multiplication of such organisms.

A compound capable of supporting growth in darkness can be overlooked in this type of study, as Lewin has pointed out (*10*). However, the present findings suggest that heterotrophy is not an important consideration in the development of the astronomical *G. breve* populations involved in Florida red-tide outbreaks.

If Florida west coast rivers do not provide direct energy sources for multiplication of *G. breve*, the organism's vitamin, trace-metal, and chelator requirements assume added ecological significance as factors potentially limiting population growth. Similar indirect evidence may be seen in extensive field data (*11*), which suggest that phosphate and nitrate are not usually growth restricting to this form in nature.

Vitamins, trace metals, and chelators may be introduced by river waters into coastal environments. Provasoli (*12*) has pointed out broad ecological implications: "It is well known that the waters near estuaries, inlets, and inshore are fertile areas; this fertility should now be considered not only in terms of phosphates and nitrogenous compounds but also of vitamins, trace metals, and chelating agents." The natural fluctuations in levels of such substances may also be a fruitful area for future study of *G. breve* and red-tide ecology.

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4 May 1962

RESEARCH AT THE U.S. BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY, BRUNSWICK GEORGIA

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The U.S. Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia, was established in 1952 to study the physical, chemical, and biological oceanographic conditions along the south Atlantic coast of the United States.

Studies are based mainly on data and material collected during nine cruises of the M/V Theodore N. Gill during 1953 and 1954. The cruises were made over an established station pattern embracing an area between Cape Hatteras, North Carolina, and the Bahama Islands, and from near shore to beyond the axis of the Gulf Stream. On each cruise the vessel traveled about 3000 miles and occupied between 80 to 90 stations. The field work developed with the assistance of the Navy Hydrographic Office, the Office of Naval Research, and the States of Georgia and Florida.

The nine published Gill cruise reports contain all of the processed basic data on physical and chemical oceanography and biology--making available to any interested agency or person every bit of basic information obtained.

Research is conducted under two major programs: life histories and systematics of the fishes along the south Atlantic coast of the U.S., and the physical and chemical oceanography of ocean waters along that coast.

Studies have been published on the early life history, distribution, and classification of a number of groups and species of fish--other papers are in press or in preparation. Published also are the results of a chemica

nechanical analysis of the bottom sediments of the work area--a study
mplished in cooperation with the Oceanographic Institute of Florida
University.

Our studies indicate that the link between the estuarine environment
he offshore Continental Shelf area (and even the Gulf Stream) is much
r with relation to pertinent phases in the life history of many species
we expected. Thus, only through studies over a broad area from the
Stream to the estuaries can the development and survival of many
ies be followed.

Our present efforts in the biological program are concentrated on
es concerned with larval forms of fish. These studies are difficult
nly because the young stages are known for very few species, but also
use the adults of many groups are poorly distinguished. In addition
is a lack of knowledge of just how many fish do inhabit the area. In
respect, we work closely with the Bureau's exploratory fishing activi-
-cooperation which is contributing very valuable data on distribution of
ies of fish and other organisms, especially bottom dwelling forms. From
arval fish studies we expect much information on early development,
ning, growth, distribution in time and space, abundance, etc.--all
ssary to an understanding of a species presence and abundance in the
.

The physical and chemical data are being further processed and
narized to make them more useful--particularly to fishery biologists.
work area is divided into three sections (northern, central, and south-
and each of these into three subsections from shore seaward, allowing
narization of conditions north and south and from inshore to offshore.
rs on temperature and salinity are in press, and one on densities is in
preparation. Papers on oxygen and the various nutrients measured
o follow.

The present staff of the laboratory is 16--8 Fishery Biologists,
alytical Chemist, 3 Aids and Technicians, 3 Clerical, and 1 Laborer.

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nparative Toxicity of 3-Trifluormethyl-4-nitrophenol (TFM) to Larval Lampreys and Eleven Species of Fishes

Vernon C. Applegate and Everett L. King, Jr.

Comparative Toxicity of 3-Trifluormethyl-4-nitrophenol (TFM) to Larva Lampreys and Eleven Species of Fishes[1]

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ABSTRACT

The tolerances of larval lampreys, rainbow trout, and 10 species of warmwater fishes to 3-trifluormethyl-4-nitrophenol (TFM), a selective lamprey larvicide, were determined in three dilution waters of different physical and chemical characteristics. Differential toxic effects of the chemical to larval lampreys and test fishes varied broadly with the species of fish. Smallmouth bass and other centrarchids were most tolerant of the chemical; walleye, yellow perch, bullheads, and white suckers were most susceptible. The toxicity of TFM to both lampreys and fishes diminished as the conductivity and alkalinity of the dilution water increased. The differential action of the chemical was retained in all waters, however.

INTRODUCTION

The discovery of the selective toxicity of 3-trifluormethyl-4-nitrophenol (TFM) to lampreys and several species of fishes has been reported by Applegate, Howell, and Smith (1958). Further laboratory tests of the biological activity of this chemical and its experimental application in streams have been described by Applegate *et al.* (1961). The latter experiments confirmed the usefulness of TFM as a selective sea lamprey larvicide and provided the basis for undertaking a program of control of the sea lamprey in the Lake Superior basin through the destruction of larval lampreys in streams. The progress of this large-scale experiment has been reported in the processed records of the meetings of the Great Lakes Fishery Commission.

Treatments with TFM of Lake Superior tributaries infested with sea lamprey larvae have now been completed, and current plans call for the application of this larvicide in streams tributary to Lake Huron and Lake Michigan. Faunal associations in the warmer streams of the latter two basins differ markedly from those encountered in Lake Superior watersheds, particularly with respect to the principal game fish. Early simulated stream tests of TFM provided only limited information on the tolerances of several warmwater species to the chemical (Applegate *et al.*, 1961). Th objective of this study was to determine mor accurately the differential toxic effects c TFM to larval lampreys and certain repre sentative warmwater fishes that will be en countered in the treatment of Lake Huro and Lake Michigan streams. In addition t larvae of the sea lamprey (*Petromyzo marinus*), the species selected for experimen tation were: Largemouth bass (*Micropteru salmoides*), smallmouth bass (*Micropteru dolomieui*), bluegill (*Lepomis macrochirus*) walleye (*Stizostedion v. vitreum*), yello perch (*Perca flavescens*), yellow bullhea (*Ictalurus natalis*), white sucker (*Catostomu commersoni*), blacknose shiner (*Notropi heterolepis*), golden shiner (*Notemigonu crysoleucas*), and fathead minnow (*Pime phales promelas*).

Rainbow trout (*Salmo gairdneri*) were als included in the tests. Although considerabl information has been accumulated on th tolerance of this coldwater species to TFM, i was considered desirable to provide a direc comparison between its responses to the com pound and those of the other fishes unde identical test conditions. The resultant data reduced for each species to an index express ing the differential toxic effects of TFM, wi permit the continued use of rainbow trout i pre-treatment bioassays as an "indicato species" even though it may not be present i a stream in which TFM is to be applied

[1] This work supported by the Great Lakes Fishery Commission.

inbow trout are desirable for this purpose they are readily obtainable from public tcheries in the area where treatments are to carried out.

BIOASSAY METHODS

Laboratory facilities and equipment were nilar to those described by Applegate, well, Hall, and Smith (1957). Animals re placed in 10-liter glass battery jars (10-h diameter), each containing 6 liters of t solution. The test jars were aerated by ans of standard stone aerators. (Vigorous ration does not decrease the concentration this non-volatile chemical.) Oxygen levels the jars during the tests were maintained at ar-saturation. Temperatures were held con-nt at 55° F. by immersion of the test jars a specially constructed water bath.

Larval sea lampreys and yellow perch were llected in the Ocqueoc River system, esque Isle County, Michigan. All other test ecies were obtained from public or com-rcial fish hatcheries as single, uniform lots fish. Ranges of total length (in inches) of test animals were as follows: Larval sea mpreys, 3.5–5.0; largemouth bass, 4.0–5.0; allmouth bass, 3.0–4.0; bluegills, 3.0–3.5; lleye, 3.0–3.5; yellow perch, 4.5–5.5; llow bullheads, 2.75–3.25; white suckers, 5–5.0; blacknose shiners, 2.25–2.75; golden iners, 3.0–4.0; fathead minnows, 2.25–2.75; d rainbow trout, 4.5–5.5.

In experiments with the smallmouth bass, uegills, yellow perch, white suckers, and inbow trout, three specimens were placed in ch test container. For the remaining ecies, including the larval lampreys, four re installed in each test jar. After the imals were tempered and acclimated to the t temperature, appropriate amounts of TFM aqueous solutions were added to produce e desired concentrations. Five simultaneous plications were made to give a total of 15 20 individuals of each species exposed at ch concentration.

The biological activity of TFM is strongly fluenced by the hardness and pH (and per-ps other properties) of the water into nich it is introduced (Applegate *et al.*, 61). For this reason, the differential toxic action of the chemical to larval lampreys and each species of fish was determined in each of three dilution waters. These waters differed sufficiently from each other in physical and chemical characteristics to encompass nearly all conditions that will be met in tributaries of Lakes Huron and Michigan. Each test water was obtained from a single source except where pronounced seasonal variations in chemical and physical properties dictated that an alternate source be used. Dilution water A was obtained entirely from Hammond Bay of Lake Huron; dilution water B was from Little Billies Creek, Cheboygan Co., Michigan; and dilution water C was from either Devils River, Alpena Co. or Trout River, Presque Isle Co., Michigan.

TABLE 1.—*Some physical and chemical properties of dilution waters used in bioassay tests of TFM*

Properties of test water	Source of dilution water		
	Dilution water A (Hammond Bay)	Dilution water B (Little Billies Creek)	Dilution water C (Devils River; Trout River)
Conductivity (μmhos/cm/18° C)	176.3	219.1	338.7
CO_2 (ppm)	1.6	3.2	5.1
Phenolphthalein alkalinity (ppm)	0.0	0.0	0.0
Methyl orange alkalinity (ppm)	95.4	141.7	203.3
pH	7.8	7.7	7.7

Supplies of the dilution waters were obtained at intervals, as needed, and each varied in its characteristics to a limited extent during the several months when tests were in progress. These changes resulted in small variations in the biological activity of TFM in the series of tests conducted with each water. Average values of the physical and chemical properties of the dilution waters are presented in Table 1.

Physical and chemical analyses of dilution waters were made immediately before their use in all tests. Procedures for these determinations were generally those set forth in the ninth edition of "Standard Methods for the Examination of Water and Sewage." TFM concentrations in all test containers were checked colorimetrically by the method described by Smith, Applegate, and Johnson (1960).

TABLE 2.—*Toxicity of TFM to larval lampreys and 11 species of fish in three dilution waters of differe conductivity and alkalinity*

[Bioassay tests conducted for a 24-hour period at a water temperature of 55° F.]

Species and dilution water	Minimum lethal dose of TFM (ppm)[1]	Maximum allowable dose of TFM (ppm)[2]	Differential toxicity expressed as ratio of concentrations	
			Each dilution water	Averag
Largemouth bass				
Dilution water A	4.0	22.0	5.5	
Dilution water B	6.0	30.5	5.1	5.1
Dilution water C	9.0	42.0	4.7	
Smallmouth bass[3]				
Dilution water A	4.0	34.5	8.6	
Dilution water B	5.0	42.0	8.4	8.5
Bluegill				
Dilution water A	4.0	21.5	5.4	
Dilution water B	6.0	30.5	5.1	5.1
Dilution water C	9.0	44.0	4.9	
Walleye				
Dilution water A	4.0	5.75	1.4	
Dilution water B	6.0	7.5	1.3	1.3
Dilution water C	10.0	11.5	1.2	
Yellow perch				
Dilution water A	4.0	7.25	1.8	
Dilution water B	5.0	13.0	2.6	2.2
Dilution water C	10.0	20.5	2.1	
Yellow bullheads				
Dilution water A	4.0	5.75	1.4	
Dilution water B	6.0	9.5	1.6	1.6
Dilution water C	8.0	15.5	1.9	
White suckers				
Dilution water A	3.0	5.0	1.7	
Dilution water B	5.0	6.75	1.4	1.5
Dilution water C	9.0	13.0	1.4	
Blacknose shiners				
Dilution water A	4.0	13.25	3.3	
Dilution water B	6.0	18.5	3.1	3.2
Dilution water C	9.0	28.0	3.1	
Golden shiners				
Dilution water A	4.0	14.75	3.7	
Dilution water B	5.0	22.5	4.5	4.0
Dilution water C	9.0	33.0	3.7	
Fathead minnows				
Dilution water A	4.0	16.0	4.0	
Dilution water B	6.0	24.25	4.0	4.1
Dilution water C	8.0	35.5	4.4	
Rainbow trout				
Dilution water A	3.0	12.0	4.0	
Dilution water B	5.0	20.75	4.1	3.8
Dilution water C	8.0	25.25	3.2	

[1] Dose required to kill 100 percent of the larval lampreys.
[2] Dose required to kill 25 percent of the test fish.
[3] Tests in dilution water C omitted as smallmouth bass will tolerate concentrations of TFM in excess of the amount the chemical that will go into solution at 55° F. in this water.

Each bioassay test lasted 24 hours.[2] The responses of the test animals were observed at 1-hour intervals during the first 8 hours and again at the 24th hour of exposure. Arithmetic dosage intervals were employed in all tests. Mortalities of larvae at the 100-percent level were determined directly from laboratory test results. Mortalities of fishes at the 25-percent level were derived from curves prepared from the mortality data.

[2] In the development of sea lamprey larvicides, bioassay test periods have never exceeded 24 hours because practical considerations of cost preclude more extended treatment periods in the field.

BIOASSAY RESULTS

Minimum lethal doses for larval lampre (concentration killing 100 percent of t larvae within 24 hours) and maximum allo able doses for the test fishes (concentrati killing 25 percent of the specimens within hours) in each dilution water are given Table 2. Differential toxic effects of the che ical to larval lampreys and the test fishes va ied broadly with the species of fish expose Rainbow trout, blacknose and golden shine and fathead minnows all exhibited appro imately the same response to TFM; *i.*

aximum allowable dosages for these species ere approximately three to four times as eat as the minimum lethal doses for mpreys. The centrarchids as a group were ore tolerant of TFM than were the trout and prinids. Outstanding among them was the nallmouth bass. Maximum allowable doses r this fish were about 8½ times the dosages quired to kill all of the lampreys. Walleyes, llow perch, yellow bullheads, and white ckers were relatively susceptible to the emical. Least tolerant was the walleye. aximum allowable dosages for this species ere only slightly greater than the concentra- ons required to kill all larvae.

The toxicity of TFM to both lampreys and shes diminished as the conductivity and al- linity of the dilution water increased; it as most toxic in dilution water A and least xic in dilution water C. The ratio of the inimum lethal dose for larval lampreys and e maximum allowable dose for a particular sh species varied little among the dilution aters. The means of the ratios therefore ovide a reasonably sound measure of con- tions to be expected in a wide variety of reams.

We feel it desirable to warn against application of our findings to the use of TFM for the selective destruction of fish species other than larval lampreys. Although the sensitivity of various fishes did differ rather widely, it would be dangerous to hold that the difference would persist in other waters. Use of TFM as a selective fish toxicant should be preceded by extensive and discriminating bioassay tests.

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LIGHT PENETRATION IN THE GREAT LAKES

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Abstract

Measurements have been made of incident and subsurface light intensities at several depths in Lakes Erie, Michigan, Huron, Ontario, and Superior. At least one study was made of the spectral distribution of ambient irradiance in each of the lakes. Blue light penetrated to the greatest depth in Lake Huron, green in Lakes Superior and Michigan, and orange in Lakes Erie and Ontario. Measurements were made of the changes in light intensities at several depths from sunrise to sunset in Lake Erie, Lake Michigan, and Frains Lake—a small inland lake. The percentage of incident irradiance at depth was greatest at sunrise and sunset in Lake Erie and Frains Lake. This situation occurs since incident irradiance is shifted towards the red end of the spectrum at sunrise and sunset. Consequently, a greater percentage of the incident light was in the orange region of the spectrum that penetrates deepest in these lakes. Shorter wave lengths penetrate to greater depths in Lake Michigan.

INTRODUCTION

The importance of solar radiation in the aquatic environment, as a source of heat, for photosynthesis by plants, and as an influence on the behavior of zooplankton and fish, has been recognized for many years. Furthermore, knowledge of the quantity and quality of irradiance according to depth is essential for estimating the absorption of solar energy and for studies of the nature of substances determining the optical characteristics of natural waters. Despite the acknowledged importance of solar radiation in the aquatic environment, only a few studies have been made of light conditions in the Great Lakes. Chandler (1942) studied the relation of light penetration to turbidity in western Lake Erie. The relationship of Secchi disc readings to photometer measurements has been investigated in Lakes Huron (Beeton 1958) and Erie (Halicki 1958). Verduin (1960) made a number of observations of light penetration in western Lake Erie. Two reports present limited information on the spectral distribution of light at depth (Beeton 1960, Putnam and Olson 1961).

The Bureau of Commercial Fisheries has recognized the need for more precise information on light conditions in the Great Lakes for many years. Light-penetration studies were initiated in 1954 and have been continued since then, whenever the opportunity and suitable conditions occurred. Only a few measurements have been made in Lakes Ontario and Superior but numerous observations have been made in the other lakes. Observations made on Frains Lake have been included in this report, since we have little information on diurnal changes in light intensity at different depths.

EQUIPMENT AND METHODS

Light-penetration measurements were made with a pair of model 856YR Weston photoelectric cells, matched for output and linearity, and a model 622 Weston microammeter. The waterproof case for the subsurface-cell and the

leck-cell case, gimbal mounted, were made by Schueler, Waltham, Massachu-setts. Seven pairs of matched Corning glass color filters were used with the photoelectric cells. The color filters were numbers 2404, 2418, 3482, 3387, 3389, and 5970; the spectral transmission of these filters was given by Corning (1948). The filters are in a series whereby each one, except number 5970, transmits a greater part of the spectrum than the preceding one. It was possible, therefore, to determine the light transmission for reasonably narrow regions of the spectrum. Data presented for the transmission of any particular wave band of light by the lake waters should be recognized as approximations, however, since a number of factors can introduce considerable error. To obtain the greatest accuracy when cutoff filters are used, measurements should be made while changes in the incident light are relatively small. Consequently, measurements should be made in the shortest possible time, preferably when the sun is at its zenith, the sky is clear, and the lake is calm. This combination of conditions occurs infrequently on the Great Lakes. Nevertheless, corrections can be made to compensate for some of the errors, if paired surface and subsurface measurements of light intensity are made, and if the percentage transmission of light through each filter, when the sun is at zenith on a clear day, is known.

A polished opal glass disc always was positioned above the color filters, as recommended by Atkins, et al. (1938). Three pairs of metal discs with the following central apertures limited the amount of light reaching the photocells: 7.5 mm, 15.0 mm, and 60.0 mm.

The photocells were originally calibrated by the Daylighting Laboratory, Engineering Research Institute, University of Michigan, in 1956. At the start of the calibrations it was discovered that linearity of calibration could not be obtained with the three aperture plates provided by the manufacturer and a cosine correction test indicated that the design of the instrument permitted an error in excess of 17.0%. This large error was primarily due to light scatter within the photometer cases. To obtain greater accuracy, two metal discs with 38.0 mm apertures were made, to replace those with the 60.0 mm apertures, and two 38.0 mm silver-plated brass rings were mounted in the space between the photocells and the overlying glass to eliminate some of the internal light scatter. The new metal discs produced the desired calibration linearity. A repetition of the cosine correction test revealed that the error had been reduced to 6.6% (Table 1). The metal disc with the smallest aperture was used in most of the light-intensity measurement in order to obtain the greatest accuracy. The cosine correction test indicates no appreciable error in the photometer readings when the sun has a zenith angle of 50° or less.

A standard lamp and optical bench were used for calibration of the photocells. A 1000-watt, T-20 General Electric lamp, with a color temperature slightly less than 3100°K, was positioned to give 500 and 1,000 foot-candles. The photocells were calibrated with the various color filters and metal discs in place and for three or four ranges of the microammeter. The relative energy values for tungsten filament lamp with a color temperature of 3098°K were given in Moon (1936). These values were equated to foot-candles; then the total number of foot-candles was determined for the spectral transmission range of each Corning glass filter. The response of the photocells, as measured by the microammeter, was calculated in terms of foot-candles per microampere. The microammeter readings alone could not be used to calculate percentage transmission, since the photoelectric cells were not equally sensitive to all wave lengths. A new photocell was put in the subsurface unit in September 1957, and the photometer was recalibrated. Response of the photocells has been rechecked against a standard lamp several times.

Table 1. Cosine Correction Test for Deck Cell of Photometer
[Metal disc with central aperture of 7.5 mm. Illumination, 200 foot-candles]

Angle of incident light	Meter reading (cosine-corrected)	Response of meter
0°	14	14
10°	14	14
20°	13	14
30°	12	13
40°	11	12
50°	9	9
60°	7	6
70°	5	3
80°	2	1
90°	0	0

Per cent error 6.6.

Procedure on the lakes involved lowering the sea-cell to predetermined depths from the side of the vessel facing the sun. The cable was marked at 1-meter intervals. The response of the microammeter was recorded in micr amperes; these readings were subsequently converted to foot-candles. All values were adjusted to compensate for the changes in the light intensity as t zenith angle of the sun changed. Observations in Lakes Erie and Huron were from the M/V *Cisco*, those in Lakes Michigan and Superior from the M/V *Sis cowet*. The M/V *Musky II* was used in Lake Ontario. Most of the studies were in the open waters of the lakes, although data for Lakes Erie and Superior were collected in the lee of Middle Bass and Madeline Islands because of the quieter waters (Table 2).

SPECTRAL DISTRIBUTION OF LIGHT ACCORDING TO DEPTH

Orange light (590-610 mμ) penetrated to the greatest depth in Lakes Eri and Ontario, and in Frains Lake. Lakes Michigan and Superior had their greatest transparency in the green (490-540 mμ) and Huron in the blue (440-490 mμ). The description of the optical properties of lake waters on the bas of relatively narrow wave bands, which penetrate to the greatest depths, can b misleading. For example, Frains Lake could be described better as having t greatest transparency in the red-orange if the wave band (610-750 mμ), which penetrated almost as deep as the 590-610 mμ wave band, is included (Fig. 1). Similarly, yellow-orange light penetrates deepest in Lakes Erie and Ontario, yellow-green in Lake Michigan, and blue-green in Huron and Superior. The data for Lake Superior may not describe the open-lake conditions since all measurements were made in the vicinity of the Apostle Islands. The spectra distribution of light at depth in open Lake Superior is probably very similar t that in Lake Huron (Fig. 1). Our data on the decrease in intensity of red light with increase in depth agree closely with those obtained by Putnam and Olson (1961) in the open waters of Superior. They found a greater penetratio of violet light (400-450 mμ), however, since 5% of the incident violet light pen trated to 10 meters, whereas we measured only 5% of the incident violet ligh (410-440 mμ) at 7 meters.

Table 2. Photometer-Station Data

Lake	Station location		Date	Time (local apparent)	Wind		Sky	Sea state	Secchi disc depth (meters)
	Latitude	Longitude			Direction	Velocity (mph)			
Huron	44°14'25"	83°14'50"	July 17, 1956	0900-1015	NNE	16	Clear	Choppy	11.6
Erie	41°41'15"	82°47'45"	Oct. 20, 1957	0630-1815	NW	25 diminishing to 5	Clear	Gentle	1.0
Michigan	44°47'30"	87°11'20"	May 7, 1958	0415-1903	SW	5-10	Partly cloudy	Gentle	. . .
Superior	46°52'45"	90°35'40"	June 4, 1959	1140-1218	WSW	18	Clear	Gentle	2.7
Ontario	43°19'00"	79°09'03"	Sept. 25, 1961	1000-1042	NE	12	Cloudy	Gentle	4.0
Frains	7.5 mi. NE Ann Arbor		July 18, 1957	0350-1954	SW	5	Clear	Calm	. . .

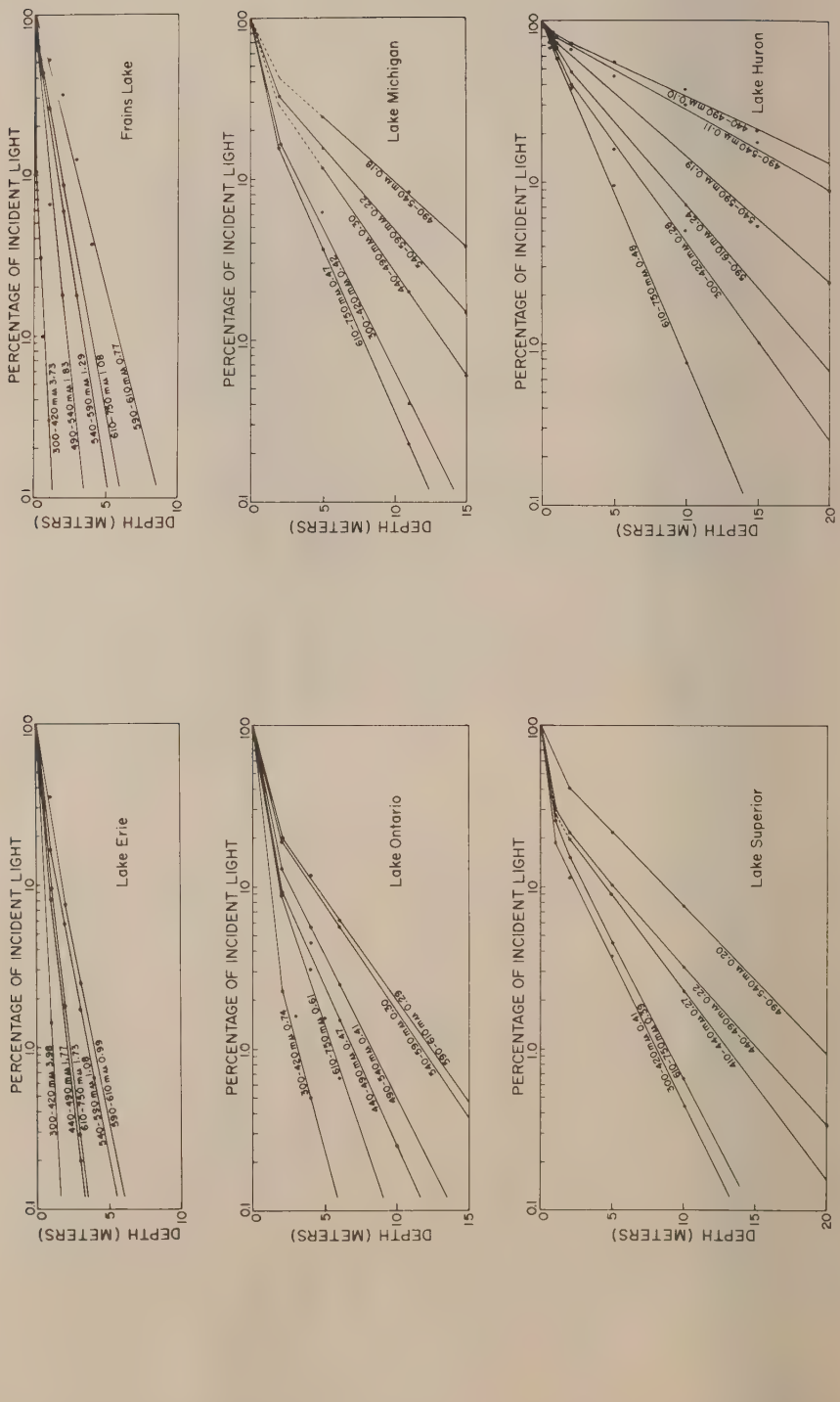

Fig. 1. Spectral distribution of light penetration (on log-log paper) in Ontario waters, following the square band classification over the graphical ordinate.

Violet (300-420 mμ) and red light (610-750 mμ) penetrated to relatively shallow depths in all the lakes (Fig. 1). Radiation in the red end of the spectrum is absorbed, however, by pure water. Pure water is very transparent to the shorter wave lengths until the far ultraviolet is reached. In natural waters, however, various materials scatter and absorb the shorter wave lengths. Consequently, the spectral distribution of light at depth is a function of the nature of water itself and the kinds and quantities of the substances in it. Blue light is scattered more by suspended materials than is light in the red end of the spectrum. Yellow organic substances absorb considerable light in the blue and ultraviolet (Strickland 1958). The concentrations of total suspended solids (Public Health Service 1959) and dissolved organic compounds in the Great Lakes increase progressively in the following sequence: Superior, Huron, Michigan, Erie, and Ontario. The spectral distribution of light at depth is in the blue-green in Lakes Huron and Superior and shifts progressively toward the red end of the spectrum in Michigan, Erie, Ontario, and Frains. The brown waters of Frains Lake have high concentrations of suspended solids and organic materials; concentrations of dissolved organic carbon are around 11 ppm (George Saunders, personal communication).

The optical properties of the various waters can best be described by vertical extinction coefficients ($\underline{K}$). This coefficient indicates the rate of decrease of light as the depth increases where:

$$\underline{K}_{\lambda} = 2.30\,(\log \underline{I}_{\lambda,h} - \log \underline{I}_{\lambda(h+1)})$$

$\underline{I}_{\lambda,h}$ and $\underline{I}_{\lambda(h+1)}$ represent the light intensity of wave length at depths h meters and (h + 1) meters. The 2.30 compensates for the use of base-10 logarithms instead of natural logarithms. This coefficient appears in the exponent of the Lambert Law. The extinction coefficients for the wave lengths penetrating to various depths in the lakes are included in Figure 1. A plot of the coefficients for their respective wave bands provides a convenient means for comparing the optical properties of the lakes (Fig. 2). Although the percentage transmission was greater for orange light (590-610 mμ) than for other wave lengths in Erie, Ontario, and Frains ($\underline{K}$ = 0.99, 0.29, 0.79), the water of the other lakes had a greater transparency for light in this wave band. The $\underline{K}$ value for the 590-610 mμ range in Lake Huron, for example, was 0.24. Data for Lake Erie are from the shallow western basin where the waters are especially turbid. The transparency as measured by a Secchi disc is usually much

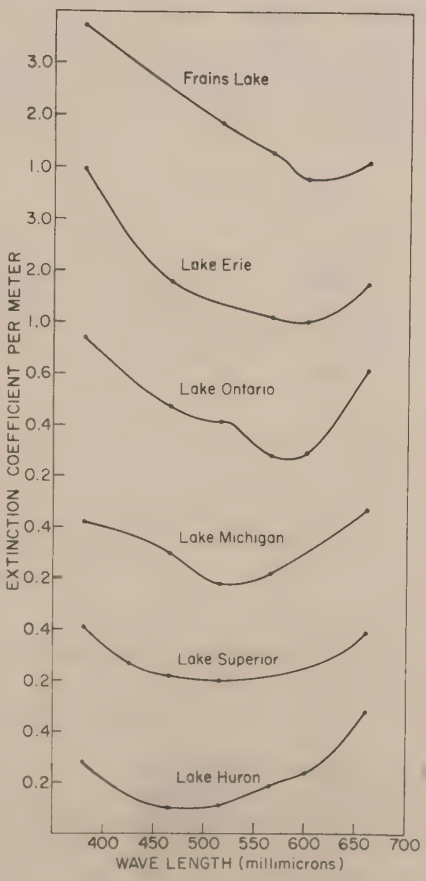

Fig. 2. Vertical extinction coefficients for various wave lengths of light in the Great Lakes and Frains Lake.

greater in the deeper waters of eastern Lake Erie. The optical properties o these waters probably are very similar to those of Lake Ontario (Fig. 2).

DIURNAL CHANGES IN LIGHT INTENSITY

Diurnal changes in light intensity were measured in Lakes Erie and Michigan and in Frains Lake at the stations where observations were made o the spectral distribution of light (Table 2). Measurements were made of inci dent light and its intensity at several depths every 15 minutes in the early morning and late afternoon, and at $\frac{1}{2}$-hour intervals during the remainder of t day.

The light-intensity curves for Lake Michigan (Fig. 3) based on a plot of intensity at various depths against time (sunrise to sunset) follow the curv for incident light very closely. Calculations of the percentage transmission o light indicate a slight increase in the percentage transmission of surface ligh from morning until noon and a corresponding decrease in the afternoon. Approximately 5% more of the surface light penetrated to 5 meters at noon than in the morning or afternoon; this change amounted to less than 2% at 10 and 15 meters. The diurnal shift in percentage transmission can be attributed to a greater loss of light from increased reflection when the zenith angle of the sun is greater than 50° (Davis 1941).

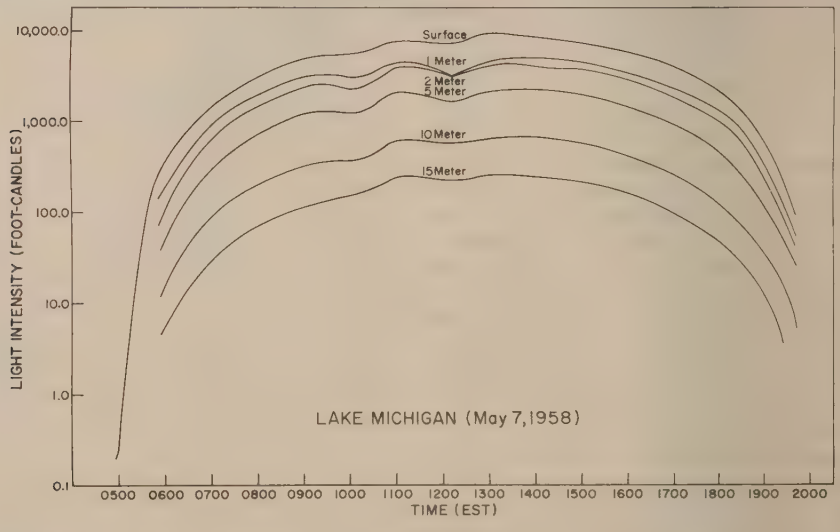

Fig. 3. Diurnal changes in incident and subsurface light in Lake Michigan.

Measurements in Lake Erie indicate that other factors were important i determining the intensity of light at different depths throughout the day. The curves for subsurface light intensity do not follow the curve for incident light as closely as in Lake Michigan but tend to flatten out in midday (Fig. 4). The increas in light intensity at depth in the afternoon was undoubtedly due to a decrease i turbidity, since the wind velocity was 25 mph until 10:00 EST and had diminished to 12 mph by 14:00 EST. The percentage of surface light at a depth of 1 meter gradually decreased from about 20% in early morning to around 16% at 10:30 EST and then increased to about 20% again in late afternoon.

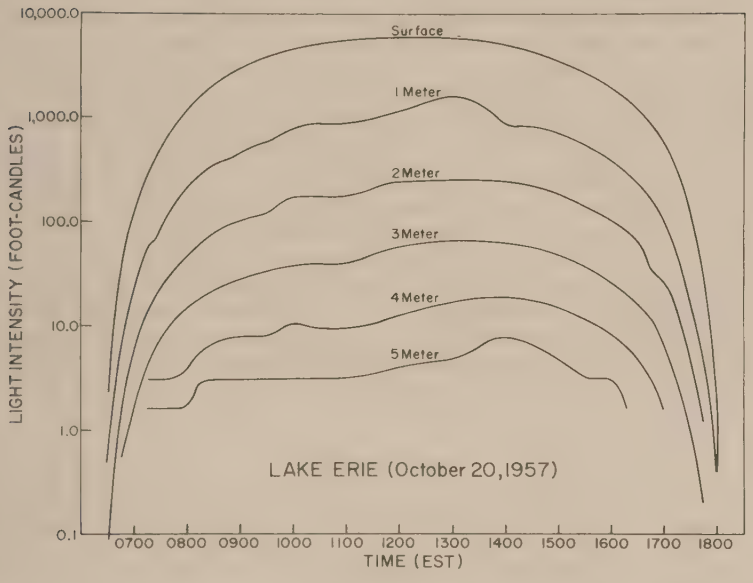

Fig. 4. Diurnal changes in incident and subsurface light in Lake Erie.

The results of observations on Frains Lake (Fig. 5) were similar to those for Lake Erie. The exact cause of the abrupt change in subsurface light intensity late in the day is not known, but it was probably due to a poor connection in the circuit. The percentage of surface light at the 1-meter depth decreased from about 17% in early morning to 11% in midday and increased again to about 16% in late afternoon.

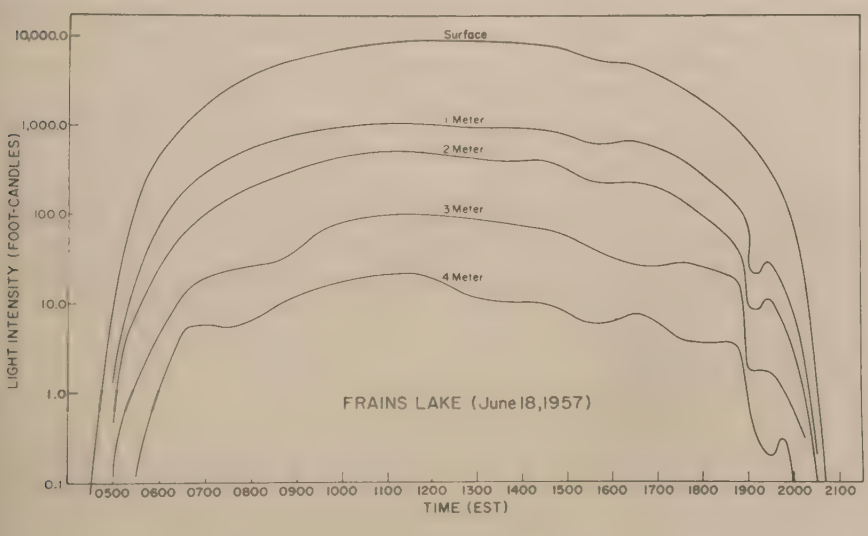

Fig. 5. Diurnal changes in incident and subsurface light in Frains Lake.

The decreases in the percentage of incident light at various depths towa midday in Erie and Frains is evidently due to the particular optical propertie of these lakes and changes in the spectrum of the incident light. These lake have the greatest transparency in the red end of the spectrum. The spectral distribution of solar energy is greatest in the red end of the spectrum when t solar altitude is 15° and shifts progressively toward the blue as the solar alt tude increases (Strickland 1958). Consequently, during early morning and late afternoon a greater percentage of the solar energy is of the wave lengths tha penetrate to the greatest depths in Lake Erie and Frains Lake. Furthermore the percentage surface loss of red light from reflection and upward scatter is less than that for total light down to zenith angles of 60° to 70° (Davis 1941). The change in the spectral distribution of solar energy with change in solar a titude may be partially responsible for the greater percentage of surface ligh at depth in midday in Lake Michigan. A greater percentage of the daylight energy is in the spectral range that penetrates deepest in Lake Michigan whe the solar altitude is 35° or more.

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Data on Six Species of Needlefishes (Belonidae) from the Western Atlantic

Frederick H. Berry and Louis R. Rivas

Data on Six Species of Needlefishes (Belonidae) from the Western Atlantic[1]

Frederick H. Berry and Louis R. Rivas

Six species of four genera of needlefishes (Synentognathi, Belonidae) occur in the western Atlantic Ocean: *Belone argala* LeSueur, *Strongylura notata* (Poey), *Strongylura timucu* (Walbaum), *Tylosurus acus* (Lacépède), *Tylosurus raphidoma* (Ranzani), and *Ablennes hians* (Valenciennes). Data are given for these species on variations in numberable characters and ontogenetic changes in morphology and morphometry. Generic relationships, species differences, and ecological notes are discussed.

THE order Synentognathi, including the Belonidae, Scomberesocidae, Hemiramphidae, and Exocoetidae, will be revised for inclusion in a forthcoming issue of the Sears Foundation series *Fishes of the Western North Atlantic*. Our investigations of western Atlantic belonids over the past several years have produced data that improve upon and clarify certain features of the taxonomy and variation, distribution, and ecology of the needlefishes in this area. This information is published at this time to encourage and promote more adequate and correct specimen identification prior to the pending revision. Because of the limited intended purpose of this paper, detailed data on measurements and counts and specimen collection data are not presented. The majority of the specimens examined that furnished data for this report are in the collections of the U. S. National Museum, the U. S. Bureau of Commercial Fisheries Biological Laboratory at Brunswick, Georgia, and the Department of Zoology Ichthyological Laboratory and Museum at the University of Miami.

The most useful publication for identifying the various species of western Atlantic Belonidae has been that of Breder (1932). We have re-examined and in certain instances re-evaluated the taxonomic characters used by Breder in his fine treatise basing our conclusions on additional material from a wider geographic area.

We are indebted to the following individuals who loaned material: Leonard P. Schultz, U. S. National Museum; Robert R. Miller, University of Michigan Museum of Zoology; John D. Kilby, University of Florida; and George S. Myers, Natural History Museum, Stanford University. Louis E. Vogele, U. S. Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia; and John S. Coles, University of Miami Ichthyological Museum, obligingly assisted in obtaining laboratory data on some of the specimens. We are grateful for review of the manuscript to Richard H. Rosenblatt, Scripps Institution of Oceanography, and Robert H. Gibbs, Jr., Boston University. For preparing Figs. 1, 2, and 3

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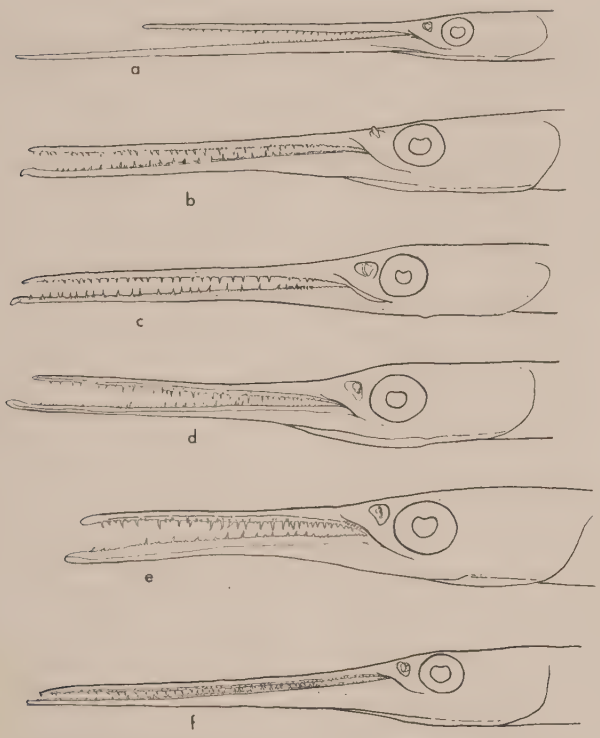

Fig. 1. a, *Belone argala,* 183 mm S.L., *Gill* Cruise 7, Std. sta., 15–16 June 1954, 2000–0100. b, *Strongylura notata,* 178 mm S.L., Sanibel Island, Florida, 17 Aug. 1959. c, *Strongylura marina,* 168 mm S.L., St. Simons Island, Georgia, 8 Aug. 1958. d, *Tylosurus acus,* 187 mm S.L., *Gill* Cruise 4, Reg. sta. 14. e, *Tylosurus raphidoma,* 202 mm S.L., *Gill* Cruise 3, Reg. sta. 51. f, *Ablennes hians,* 232 mm S.L., *Gill* Cruise 7, Reg. sta. 7.

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Generic Relationships

We recognize four genera in the western Atlantic Ocean: *Belone* Cuvier 1817, *Strongylura* van Hasselt 1823, *Tylosurus* Cocco 1833, and *Ablennes* Jordan and Fordice 1886 (the genus *Potamorrhaphis* Günther 1866, reported from fresh waters of the Guianas and Brazil is not considered here). The following are significant generic characters. Gillrakers—present in *Belone;* absent in *Strongylura, Tylosurus,* and *Ablennes.* Caudal Peduncle—strongly depressed dorso-ventrally and forming a pronounced keel in *Belone,* not dorso-ventrally depressed and usually as deep as wide in *Strongylura* and *Tylosurus* and deeper than wide in *Ablennes.* Head and Body—strongly compressed laterally and deeper than wide in *Ablennes;* not so compressed and usually as wide as deep in *Belone, Strongylura,* and *Tylosurus.* Dorsal Fin—all genera with an anterior lobe; posterior rays forming a melanistic lobe longer than the anterior lobe in juveniles and subadults of *Tylosurus* and *Ablennes* (this posterior lobe later degenerating with growth); no such posterior lobe formed in *Belone* and *Strongylura.* Upper and Lower Jaws—develop allometrically in all genera with the lower jaw relatively greatly produced at first and the upper jaw subsequently growing faster to nearly equal the length of the lower; but this phase of development is essentially completed (with the jaws becoming nearly equal) in the early juvenile stages of *Strongylura* and *Tylosurus* (more pro-

tracted in *T. acus*), while persisting to around 300 mm S.L. (standard length) in *Belone* and *Ablennes*. Dorsal Rays—less than 20 in *Belone* and *Strongylura;* more than 20 in *Tylosurus* and *Ablennes*.

Species Taxonomy

We recognize six western Atlantic species of belonids: *Belone argala* LeSueur, 1821, *Strongylura notata* (Poey, 1861), *Strongylura marina* (Walbaum, 1792), *Tylosurus acus* (Lacépède, 1803), *Tylosurus raphidoma* (Ranzini, 1842), and *Ablennes hians* (Valenciennes *in* Cuvier and Valenciennes 1846) (Fig. 1). Several other nominal species are recorded from the western Atlantic, but we have been unable to distinguish more than the above species after examining many specimens from various localities, and we regard these nominal species as synonyms of the six species we have recognized.

Belone argala has at times been confused with *Strongylura marina*. Hildebrand (*in* Longley and Hildebrand 1941:28) recorded this species as *Strongylura timucu* Walbaum, 1792. Breder (1932:12) described a new species from Tortugas, Florida, that was very similar to *B. argala*. Breder's species, described under the name of *Strongylura longleyi*, may be a valid species—we have not seen the type specimens—but we record is as a synonym of *B. argala* because all of the large number of specimens that we have examined are referable to a single species; and we think *B. longleyi* is actually a variant of *B. argala*. *B. longleyi* was reported to have less of a lower jaw extension than *B. argala* (at comparable sizes). This character cannot be used on over half of the specimens we have examined because these have portions of one or both jaws broken and missing. Of the specimens that have both jaws intact, however, those larger than 90 mm S.L. apply to Breder's concept of *B. argala* (smaller specimens are intermediate in this character, as portrayed by Breder). In the other characters that have been used to separate these two nominal species (head length, depth, and width, body depth and width, and eye diameter) we obtained an overlap of all the numerical values that have been proposed for separation, even in those specimens that can be identified as *B. argala* on the basis of relative length of the jaws.

Strongylura marina has frequently been recorded under the name of *S. timucu*. These two names were proposed on th same page by Walbaum on the basis o drawings of specimens from New York an Brazil. We have examined specimens fro Connecticut to Brazil that we regard as co specific. The specimens in the single co lection examined from Brazil (29 specimen 97.5 to about 288 mm S. L., Stanford Un versity 51795) averaged slightly less in hea and body depth and width than more nort ern specimens, but otherwise were ide tical. Re-examination of the Tortugas spec mens recorded by Breder (1932:7) as *timucu* (4 specimens, about 149 to 173 m S.L., University of Michigan 55567) show them all to have 16 dorsal rays, and 17 t 19 anal rays, while in all the anal origin 4 rays in advance of the dorsal. These cha acters are all indicative of *S. marina*.

Comparison of a large series of specime of *S. marina* from Brunswick, Georgia, wit series from Cedar Keys on the Gulf coa of Florida shows slight average difference between these two groups in several cha acters (depth vs. width, eye diameter, upp and lower jaw lengths, and pigmentation) but these differences all overlap and do n indicate even subspecific differentiation. E amination of specimens from Jamaica, i cluding the type of *S. euryops* (Bean an Dresel, 1884), shows them to have slightl broader heads and beaks, larger eyes, an shorter jaws than specimens of *S. marin* from mainland collections, but these mino differences are not sufficient to warra their recognition as two distinct species. W believe that at present there is little, if an gene flow between the insular and co tinental populations, but that they aros from a common stock and have not diverge at the species level.

In *Strongylura notata* we have observe slight differences between specimens from th east and the west coasts of Florida, and the are slight differences between specimens fro insular collections and from collections fro continental waters. We believe this to b simply intraspecific geographic variatio and the same reasoning applied to variatio in *S. marina* may be applied to *S. notat S. notata* has probably been confused o occasion with *S. marina*—this opinion base on inadequate key characters given by som previous authors.

Tylosurus acus and *T. raphidoma* are di tinctively different from each other in the

younger stages, but the characters which separate them become less well defined as development progresses.

Ablennes hians is very distinctive and should not be confused with any other Atlantic species except possibly one of the species of *Tylosurus* at very small sizes.

Two characters previously used for interspecific distinctions—number of scales, predorsal or along the body, and presence or absence of a peduncular keel (in species other than *Belone argala*)—are not used here because the randomly inserted scales form no definitive pattern and are most difficult to count, and the so-called peduncular keel formed by the expanded lateral line scales varies intraspecifically with growth and with the nature of preservation of the specimen.

Synonymies

Belone argala: *Belone argalus* LeSueur, 1821 (Guadeloupe, West Indies); *Belone ardeola* Valenciennes *in* Cuvier and Valenciennes, 1846 (Porto Rico); *Belone microps* Günther, 1866 (Surinam, British Guiana); ? *Strongylura longleyi* Breder, 1932 (Key West, Florida).

Strongylura notata: *Belone notata* Poey, 1861 (Cuba); *Strongylura notata forsythia* Breder, 1932 (Lake Forsyth, Andros Island, Bahamas).

Strongylura marina: *Esox marinus* Walbaum, 1792 (New York); *Esox timucu* Walbaum, 1792 (Brazil); *Esox longirostris* Mitchill, 1818 (Hudson River); *Belone truncata* LeSueur, 1821 (New York Bay); ? *Belone almeida* Quoy and Gamaird, 1824 (Bay of Rio de Janeiro); ? *Belone cigonella* Valenciennes *in* Cuvier and Valenciennes, 1846 (Porto Rico); ? *Belone galeata* Valenciennes *in* Cuvier and Valenciennes, 1846 (Cayenne); ? *Belone scutator* Girard, 1859 (Brazos Santiago; St. Joseph Island, Texas); *Belone subtruncata* Poey, 1860 (Havana); *Belone depressa* Poey, 1860 (Cuba); ? *Belone diplotaenia* Cope, 1871 (St. Martins, West Indies); *Tylosurus euryops* Bean and Dresel, 1884 (Jamaica); *Tylosurus sagitta* Jordan and Gilbert, 1884 (Key West, Florida).

Tylosurus acus: *Sphyraena acus* Lacépède, 1803 (Martinique); *Belone caribbaeus* LeSueur (Caribbean Sea); *Belone latimana* Poey, 1861 (Havana); *Belone altipinna* Poey, 1861 (Cuba); ? *Belone jonesi* Goode, 1877 (Bermuda).

Tylosurus raphidoma: *Belone raphidoma* Ranzani, 1842 (Brazil); *Belone gerania* Valenciennes *in* Cuvier and Valenciennes, 1846 (Martinique); *Belone crassa* Poey, 1861 (Cuba); *Belone melanochira* Poey, 1861 (Cuba); *Tylosurus gladius* Bean, 1882 (Pensacola, Florida).

Ablennes hians: *Belone hians* Valenciennes *in* Cuvier and Valenciennes, 1846 (Bahia, Havana); *Belone maculata* Poey, 1861 (Cuba).

Key to Western Atlantic Belonidae

A. Dorsal rays 12–17 ..... B.
AA. Dorsal rays 21–26 ..... D.
B. Gillrakers present. Caudal peduncle strongly compressed dorso-ventrally ..... *Belone argala.*
BB. No gillrakers. Caudal peduncle not compressed dorso-ventrally ..... C.
C. Ventral margins of maxillaries not covered by preorbitals. Anal rays 16–20 ..... *Strongylura marina.*
CC. Maxillaries completely covered by preorbitals. Anal rays 13–16 ..... *Strongylura notata.*
D. Anal rays 25–28. Head and body strongly compressed laterally. [Head width 2.6–3.5 per cent S. L. in specimens larger than 80 mm S. L.] ..... *Ablennes hians.*
DD. Anal rays 19–23. Body not strongly compressed laterally ..... E.
E. Head width 3.4–4.2 per cent S. L. in specimens larger than 100 mm S. L. Head depth 4.1–5.4 per cent S. L. in specimens larger than 60 mm S. L. Lower jaw length 22.4–23.8 per cent S. L. in specimens larger than about 170 mm. Lower jaw extension 1.6–3.7 per cent S. L.; usually 2.0–3.1 per cent S. L. in specimens smaller than 150 mm S. L. Anal lobe length 5.5–6.2 per cent S. L. ..... *Tylosurus acus.*
EE. Head width 5.0–6.0 per cent S. L. in specimens larger than 100 mm S. L. Head depth 5.5–6.8 per cent S. L. in specimens larger than 60 mm S. L. Lower jaw length 18.8–21.8 per cent S. L. in specimens larger than about 170 mm. Lower jaw extension 0.5–1.6 per cent in S. L. in specimens smaller than 150 mm S. L. Anal lobe length 7.5–9.2 per cent S. L. ..... *Tylosurus raphidoma.*

TABLE 1. COMPARISON OF DORSAL AND ANAL FIN RAY COUNTS FOR WESTERN ATLANTIC BELONIDA
Belone argala (a), *Strongylura notata* (n), *Strongylura marina* (m), *Tylosurus acus* (a′), *Tylosurus raphidoma* (r), AND *Ablennes hians* (h)

Anal Rays \ Dorsal Rays	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
13		n													
14		n	n	n											
15		n	n	n											
16			n m	m											
17	a	a	m a	m	m										
18	a	a	m a	m a	m										
19		a	a	m	m	m					r				
20						m				a′	a′	r a′			
21											r a′	r a′	r a′	a′	
22													r a′	a′	
23														a′	
24															
25													h	h	
26												h	h	h	h
27													h	h	h
28															h

ANALYSIS OF CHARACTERS

DORSAL AND ANAL FIN RAYS

The correlations of dorsal and anal fin ray counts are shown in Table 1. *A. hians* is completely separable from the other species in having more anal rays (25 to 28). *T. acus* and *T. raphidoma* average almost as many dorsal rays as *A. hians,* but have fewer anal rays (19 to 23); these two species are completely separable from *S. notata, S. marina,* and *B. argala* in having larger numbers of dorsal rays (21 to 25); *T. acus* averages one more dorsal and anal ray than *T. raphidoma,* but the total counts overlap. *S. notata* averages the least number of anal rays and is separable from *B. argala,* but overlaps *S. marina* in this character. *B. argala* averages a fewer number of dorsal rays than *S. marina,* but the ranges overlap. *T. rap*
idoma and *T. acus* have more dorsal ra
than anal rays, while the other four speci
(with the exception of one specimen of
notata) have fewer dorsal rays than an
rays, or the numbers are equal.

The first several rays of the dorsal ar
anal fins may be unbranched; this is usual
only the first and second rays in specime
smaller than about 250 mm S. L., and on
the first ray in larger specimens. Howeve
as many as the first five rays may be u
branched in specimens as small as 150 m
S. L. The last ray is more deeply branche
than the others, but it is never branched
its base—this terminal ray is counted as
single element. All the dorsal and anal f
rays of juvenile and adult specimens of
argala, S. notata, and *S. marina* are se

Table 2. Numbers of Specimens with Pectoral Ray Counts Recorded from Both Sides of each Fish

Species	Pectoral Fin Ray Counts from Both Sides of Each Fish										
	10–10	10–11	11–11	11–12	12–12	12–13	13–13	13–14	14–14	14–15	15–15
Belone argala			26								
Strongylura notata	2	3	31	9	5						
Strongylura marina	1	0	61	2	8						
Tylosurus acus							14	4	8		
Tylosurus raphidoma								1	8		
Ablennes hians									27	0	2

mented; the first dorsal and anal rays of *T. acus, T. raphidoma,* and *A. hians* may remain unsegmented in specimens up to 300 mm S. L., but all dorsal and anal rays of these three species are usually segmented above this size.

Relation of Dorsal Fin Origin to Anal Fin Origin

The origin of the dorsal fin is either in front of the anal fin origin or over one of the first seven rays of the anal fin. It is in front of or over the first or second (usually the first) ray in *S. notata*; in front of or over one of the first three anal rays (usually the first) in *T. raphidoma*; over the second, third, or fourth (usually the third) ray in *T. acus;* over one of the second through the sixth (usually the fourth) rays in *S. marina*; over the fourth, fifth, or sixth (usually the fifth) ray in *B. argala*; and over the fifth, sixth, or seventh (usually the sixth) ray in *A. hians.*

Pectoral Fin Rays

Pectoral rays were counted on both sides of the fish. In the relatively few instances where different counts were obtained for the two fins of a fish, the side having the higher number seemed to be randomly right or left. The counts are recorded in Table 2. In most juveniles and adults the first and the last one or two pectoral rays are unbranched, although in smaller specimens the first two and the last three to five rays may be unbranched. All of the pectoral rays are segmented.

Pelvic Fin Rays

Pelvic fin ray counts were made on a large number of specimens of each species. The rays numbered six in all of the specimens counted. In specimens larger than 200 or 300 mm S. L. all of the pelvic rays are usually branched, but in specimens smaller than 200 mm S. L. the first ray is usually unbranched. All of the pelvic rays are segmented.

Gillrakers

Gillrakers are present in all specimens of *Belone argala* examined from 34.5 to 322 mm S. L. They were absent in the other five species (except that minute tubercles were present on the first gill arch of a 43-mm S. L. specimen of *Ablennes hians*). The number of definitive rakers on the first gill arch of *B. argala* ranged from 1 to 5 on the upper limb and 4 to 9 on the lower limb. Small, scarcely countable rudiments are present anterior to these on both limbs. The definitive gillrakers seem to reach their maximum development in number and relative size between about 100 and 200 mm S. L.

Maxillary and Preorbital Bones

In *Strongylura marina* the ventral margin of the maxillary bone on each side of the mouth is exposed below the lower margin of the preorbital bone. In the other five species the maxillaries are completely covered by the preorbitals when the mouth is closed (Fig. 1).

Peduncular "Keel"

The peduncle of *B. argala* is very strongly depressed, dorso-ventrally, forming a bilateral keel. This keel had not formed on an 18.8-mm specimen, but was developed on the next largest specimen examined, 34.5 mm S. L. The ratio of peduncle depth into peduncle length for specimens of *B. argala* from 61.5 to 256 mm S. L. is about 2.0 to 2.7. The other species lack such a definitive keel, although the lateral line scales on the peduncle may be enlarged to produce a raised line along the sides of the peduncle. The

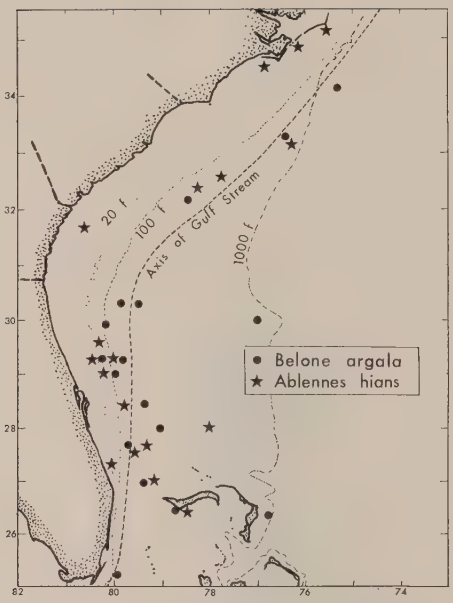

Fig. 2. Locations of capture of specimens of *Belone argala* and *Ablennes hians* recorded in this study.

ratio of peduncle depth into peduncle length for *S. notata, S. marina, T. raphidoma,* and *T. acus* ranges from about 0.9 to 1.2. The laterally compressed body of *Ablennes hians* is reflected in the compression of the peduncle which has a ratio of depth into length of 0.6 to 0.7.

Body Proportions

Standard length (measured from tip of snout or upper jaw to caudal base or end of hypural bones): Standard length is symbolized in the text as S. L.

Head length (from tip of snout to posterior end of operculum): The head length of all species increases relative to the standard length with growth of the fish, especially in *B. argala. S. notata* and *S. marina* tend to have the greatest head length; and above about 50 mm S. L., *S. marina* and *S. notata* (33.4–43.5% S. L.) are separable from *T. acus* and *T. raphidoma* (27.5–33.2% S. L.) by this character.

Head depth (vertical measurement through posterior margin of orbit): *B. argala* tends to have the least head depth; above about 60 mm S. L. *B. argala* (3.0–5.0% S. L.) and *T. acus* (4.1–5.4% S. L.) have a lesser head depth than does *T. raphidom* (5.5–6.8% S. L.).

Head width in head depth (ratio): *A hians* (1.41–1.76) has a higher ratio for th character than the other 5 species (0.88 1.40).

Snout length (tip of snout to anteric margin of orbit): The snout of all specie increases in length relative to the standar length with growth of the fish. *S. notat* tends to have the greatest snout length and above about 80 mm S. L., *S. notat* (23.3–30.3% S. L.) can be distinguishe from *T. acus* and *T. raphidoma* (16.6–22.9% S. L.) by this character.

Lower jaw extension (tip of lower jaw t tip of upper jaw): The lower jaw extensio in all species tends to decrease with respec to standard length with growth of the fis and at sizes larger than about 150 mm S. L the lower jaw extension is very small. *A argala* has the greatest extension and tha of *A. hians* is next. At sizes smaller tha 159 mm S. L., *T. raphidoma* (0.5–1.6% S. L.) has, on the average, a shorter lowe jaw extension than *T. acus* (1.6–3.7% S. L.)

Eye diameter (greatest horizontal diamete of orbit): The eye of all species tends to de

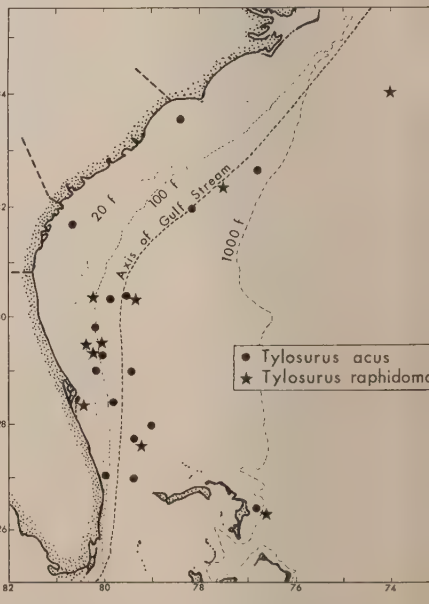

Fig. 3. Locations of capture of specimens o *Tylosurus acus* and *Tylosurus raphidoma* re corded in this study.

crease in relative diameter with growth. *S. notata* (3.8–6.4% S. L.) tends to have the largest eye, that of *S. marina* is only slightly smaller, and *A. hians* (2.5–3.7% S. L.) has the smallest eye.

Postorbital head length (posterior margin of orbit to posterior margin of operculum): *B. argala* and *A. hians* (5.6–8.1% S. L.) have the shortest postorbital head length; *S. notata* and *S. marina* (8.2–13.5% S. L.) have the highest average values for this character.

Dorsal lobe length (origin of longest dorsal fin ray to its tip): The second or third (rarely the fourth) ray is the longest at all body lengths in *B. argala, S. notata,* and *S. marina.* In the other three species, the second or the third ray is usually the longest ray of the fin at the largest body sizes, but in smaller specimens the posterior rays are produced into a melanistic lobe that tends to be longer than the anterior lobe. In such specimens, the 17th to the 19th rays are the longest in *T. acus,* the 17th to the 20th in *T. raphidoma,* and the 19th to the 23rd in *A. hians.* This posterior lobe will degenerate with growth—the degeneration in *T. raphidoma* has been described by Breder and Rasquin (1952). The anterior lobe becomes longer than the posterior lobe between about 450 and 500 mm S. L. in *T. acus,* between about 200 and 250 mm S. L. in *T. raphidoma,* and possibly at about 300 mm S. L. in *A. hians.* Considering relative lengths of the anterior lobe, those of *S. notata* and *T. raphidoma* (6.7–8.4% S. L.) tend to be longer than those of the other 4 species (3.9–6.7% S. L.).

Anal lobe length (origin of longest anal ray to its tip): The second ray is usually the longest, but often the third, and rarely the fourth may be longest. *T. acus* and *A. hians* (4.5–6.2% S. L.) have shorter anal lobes than *S. notata, S. marina,* and *T. raphidoma* (6.5–9.3% S. L.).

Dorsal base length (origin of dorsal fin to posterior margin of insertion of last ray): *T. acus, T. raphidoma,* and *A. hians* (16.0–21.5% S. L.), the species with the greatest number of dorsal fin rays, have longer dorsal fin bases than the other three species (8.8–13.8% S. L.).

Anal base length (origin of anal fin to posterior margin of insertion of last ray): *T. acus, T. raphidoma,* and *A. hians* (15.6–19.9% S. L.) have longer anal fin bases than the other three species (9.8–15.2% S. L.).

Anal base in dorsal base (ratio): This ratio is lower in *B. argala, S. marina,* and *A. hians* (0.73–0.97), species with the anal fin base longer than the dorsal fin base, than in *S. notata, T. acus,* and *T. raphidoma* (1.02–1.25), in which the dorsal base is longer than the anal base.

Pectoral length (dorsal margin of pectoral insertion to tip of longest ray): *S. notata* (8.5–10.8% S. L.) tends to have a longer pectoral fin than the other five species (5.1–9.6% S. L.).

Pelvic length (lateral margin of pelvic insertion to tip of longest ray): At sizes larger than about 100 mm S. L., *T. raphidoma* (6.6–7.8% S. L.) has a longer pelvic fin than the other five species (3.4–5.9% S. L.).

Pelvic length in pectoral length (ratio): The ratio tends to decrease in value with increase in body length. For specimens larger than about 90 mm S. L., *T. acus* and *T. raphidoma* (1.07–1.40) have a lower ratio than the other four species (1.33–2.39).

Pectoral to pelvic distance (dorsal margin of pectoral fin insertion to lateral margin of pelvic fin insertion): *S. marina* (25.3–28.2% S. L.) tends to have the pelvic fin inserted closer to the pectoral fin than in the other five species (26.5–34.8% S. L.).

Pelvic to caudal base distance (lateral margin of pelvic fin insertion to middle of caudal base): Largely as a reflection of its greater snout length, in *S. notata* (28.3–32.4% S. L.) this distance is less than in the other five species (31.7–43.0% S. L.).

Pelvic-to-caudal distance in pectoral-to-pelvic distance (ratio): This ratio is higher in *S. notata* (0.92–1.03) than in the other five species (0.64–0.88).

Ecological Notes

Strongylura notata and *S. marina* are primarily inshore species, inhabiting shallow waters of the American continents and being fairly closely confined to islands in the West Indies. *S. marina,* at least, ascends freshwater rivers and associated lakes. These species both probably spawn inshore. It is probable that the populations of these two species along the mainland of the American continents are completely isolated from the insular populations of the West Indies, and in fact the continental populations of each may be comprised of a number of sub-populations over their long ranges. By contrast, *Belone argala* and *Ablennes hians* are primarily offshore species and are only in-

frequently taken in inshore collections. *Tylosurus acus* and *T. raphidoma* occur in inshore waters more frequently than *B. argala* and *A. hians,* but their primary habitat may also be offshore. These last four species are probably pelagic spawners in offshore waters, and their inshore occurrences seem to be more common around islands than on the mainland. The concentrated dip-net collecting from near the beaches to beyond the axis of the Gulf Stream off the east coast of Florida, Georgia, and the Carolinas by the *Theodore N. Gill, Combat,* and *Silver Bay* (research vessels of the U. S. Bureau of Commercial Fisheries) produced specimens of *Strongylura* only from inshore stations while specimens of *Belone, Tylosurus,* and *Ablennes* were mainly taken well out in the Gulf Stream (Figs. 2 and 3).

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U. S. Bureau of Commercial Fisherie Biological Laboratory, Brunswick Georgia, and Ichthyological Labora tory and Museum, Department of Zo ology, University of Miami.

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BLOOD CELL TYPES AND DIFFERENTIAL CELL COUNTS IN ATLANTIC HERRING, *CLUPEA HARENGUS HARENGUS*.—Gulf of Maine and Bay of Fundy herring are difficult to age with the usual methods (i.e., length frequency, scale, otolith, and fin ray analysis), and new approaches are currently being tried. One approach is to determine if qualitative and/or quantitative differences in blood cells are discernible in herring of different lengths. This note describes the various cell types and their frequency of occurrence in herring of three length groups.

Blood samples were obtained from brit (75 to 100 mm), juvenile (101 to 200 mm), and adult Atlantic herring (201 to 290 mm) from Cape Porpoise and Kennebunkport, Maine; Stellwagen Bank; and Yarmouth, Nova Scotia. Blood was drawn as described by Perkins (1957, *Prog. Fish Cult. 19:144*), and prepared for Giemsa staining as suggested by Kolmer, Spaulding, and Robinson (1951, *Approved laboratory techniques, 5th edition, Appleton–Century Crofts, Inc. New York 72–80*) using 95 per cent alcohol as a fixative. Observations were made under oil immersion at a magnification of 1,445 diameters. Measurements were made by an eyepiece micrometer, and the differential determinations by averaging 5 vertical and 5 horizontal slide counts.

Eight types of blood cells were recognized: immature erythrocytes, mature erythrocytes, ghost cells, lymphocytes, spindle cells, eosinophils, basophils, and neutrophils (Fig. 1). The size range and distinguishing features of the blood cell types are described in Table 1. The per cent frequency of the cell types in the three length groups and the per cent of each type in ripe and spent adult males and females are presented in Table 2.

These types agree, with two exceptions, with Catton's (1951, *Blood. 6:30–60*) description of blood cells of the brown trout, common roach, and perch. He did not describe eosinophils but did report the presence of granular anucleated bodies. Naumov (1960 Translation. *U. S. Fish and Wildl. Serv. Spec. Sci. Rept. Fish. (327):203–62*) on the other hand, reported finding eosinophils but no basophils in the blood cells of Murmansk herring.

The dimensions of the lymphocytes examined agree with those reported by Naumov for the Murmansk herring, while the eosinophil and neutrophil measurements exceed those of the Murmansk herring (eosinophils by 2 microns; neutrophils by 5 microns).

TABLE 2. PER CENT FREQUENCY OF BLOOD CELL TYPES (EXCLUSIVE OF MATURE ERYTHROCYTES) IN THE ATLANTIC HERRING, *Clupea h. harengus*, OF 3 DISTINCT SIZE GROUPS. NUMBER OF SAMPLES EXAMINED INDICATED IN PARENTHESES. THESE CELL TYPES COMPRISE LESS THAN 3 PER CENT OF THE TOTAL BLOOD COUNT

Cell Types	Length Range					
	75 to 100 mm (12)	101 to 200 mm (15)	201 to 300 mm			
			Males		Females	
			Ripe (15)	Spent (16)	Ripe (14)	Spent (13)
Immature erythrocytes	10	12	37	29	27	20
Ghost cells	50	22	20	17	46	29
Lymphocytes	17	28	12	15	20	19
Spindle cells	1	4	7	3	0	4
Eosinophils	2	2	1	2	1	1
Basophils	19	31	22	30	5	25
Neutrophils	1	1	1	4	1	2

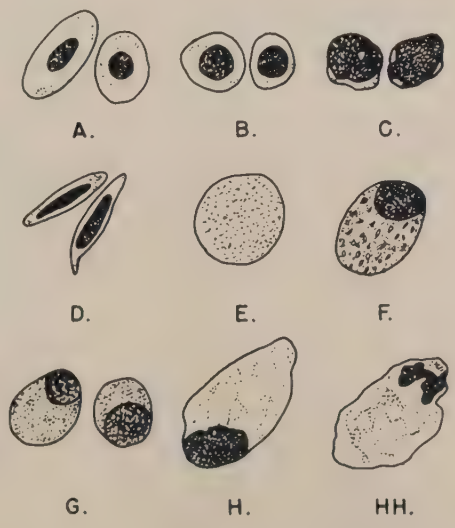

Fig. 1. Line drawings of blood cell types of *Clupea harengus harengus* (not drawn to scale—see Table 1). A. Mature erythrocyte. B. Immature erythrocyte. C. Lymphocyte. D. Spindle cell. E. Ghost cell. F. Eosinophil. G. Basophil. H. Neutrophil. HH. Neutrophil with bilobed nucleus.

TABLE 1. SIZE RANGE AND DISTINGUISHING FEATURES OF THE BLOOD CELLS OF THE ATLANTIC HERRING, *Clupea harengus harengus*

Cell Types	Number Cells Examined and Measured	Appearance in Giemsa Stain		Size of Nucleus and Cells in Microns			
				Nucleus		Entire Cell	
		Nucleus	Cytoplasm and Cell Outline	Range	$\bar{x}$	Range	$\bar{x}$
Immature erythrocytes	100	Circular; varies from dark bluish-red to purple; takes up major portion of cell.	Circular or somewhat elliptical; varies from light blue to pale green; granules distributed randomly throughout cytoplasm.	3×3	3×3	4×4 to 5×5	5×4
Erythrocytes	100	Elliptical and often takes shape similar to entire cell; varies from a dark bluish-red to purple; observed most frequently in center of cell.	Varies from circular to elliptical; varies from pale white (clear) to pale bluish-green; granules distributed randomly throughout cytoplasm.	3×2 to 4×3	4×2	6×5 to 11×8	9×7
Ghost cells	100	NONE	Varies from oval to circular; varies from pale to dark red; no diffusion of nuclear material into cytoplasm.			8×8 to 11×10	10×9
Lymphocytes	100	Irregularly elliptical; varies from dark red to light purple. On occasion will appear a dark blue; takes up almost entire cell.	Irregularly elliptical; white (clear) to pale blue; very little cytoplasm.	3×3 to 5×3	4×3	4×4 to 6×4	5×4
Spindle cells	25	Elongate elliptical; varies from dark red to light purple; takes up almost entire cell.	Elongate elliptical and tapering at ends; varies from clear to light pink; granules evenly distributed throughout cytoplasm.	4×2 to 5×2	4×2	8×4 to 12×3	10×3
Eosinophils	20	Oval; varies from dark red to light purple; observed most frequently at extreme end of cell.	May be elliptical, oval, or circular; mottled blue; large red granules appear in cytoplasm.	5×4 to 7×4	5×5	10×10 to 14×12	12×10
Basophils	25	Oval or elliptical; varies from bright red to reddish purple; observed most frequently at either extreme end of cell.	Varies from oval to irregularly circular; light blue; coated fine purple granules which give the cytoplasm the appearance of being dark blue in the large cells and purple in the small cells.	4×4 to 5×4	4×4	8×8 to 14×13	11×10
Neutrophils	20	Irregular elliptical; may be bilobed; varies from blue to purple; observed most frequently at extreme end of cell.	Irregularly elliptical; clear to very pale blue; extremely fine granules dispersed occasionally to give appearance of irregular rows.	7×6 to 10×9	9×8	18×11 to 24×16	19×13

In the samples examined there were no
fferences in the occurrence of the various
ll types that related to length, or that
ffered any promise as an aging method.—
. C. Boyar, *Bureau of Commercial Fish-
ies Biological Laboratory, Boothbay Har-
or, Maine.*

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OCCURRENCE OF SCUP, *Stenotomus versicolor*, IN MAINE WATERS IN NOVEMBER

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On November 30, 1961 a scup, *Stenotomus versicolor*, was caught in an otter trawl from the Bureau of Commercial Fisheries research vessel *Phalarope*. The catch was made in 80 feet of water in the Sheepscot River at latitude 43°54′48″ N and longitude 69°41′25″ W (near Boothbay Harbor, Maine). The specimen was 4 7/16 inches in total length and weighed 0.33 ounces.

According to Bigelow and Schroeder (1953, U. S. Fish. Wildl. Ser., Fish. Bull. 74(53) : 415), scup leave the inshore waters in the early fall and migrate offshore where they remain until the spring. These authors reported that Cape Ann, Massachusetts was the northern boundary to the usual range of scup, although small catches had been landed in Lincoln County, Maine and as far north as Eastport, Maine. More recent northern records are those of Leim and Day (1959, Jour. Fish. Res. Bd. Canada, 16(4) : 510) and Leim (1960, Jour. Fish. Res. Bd. Canada, 17(5) : 732) who reported scup from Passamaquoddy Bay, New Brunswick, and St. Mary's Bay, Nova Scotia. However, all their specimens but one (a 9 3/8-inch scup caught on December 10) were taken prior to October 16. Several Maine coast fishermen, when interviewed, had no recollection of scup occurring in their trap or otter trawl catches after late October. Therefore, the presence of the species in Maine inshore waters in late November is rare.

The only other observation of scup occurring in Maine waters after October was made by Gareth W. Coffin of the Bureau of Commercial Fisheries Biological Laboratory, Boothbay Harbor, Maine. He identified a 11 3/8-inch specimen caught in the Boothbay Harbor area by a local fisherman during the second week of November, 1957.

The size of the 4 7/16-inch specimen suggests it was spawned in 1961 spawning, possibly in the Boothbay Harbor area.

after Bigelow and Schroeder

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On the Nature of the Selective Fishing Action of Longline Gear

VERNON E. BROCK[1]

HERY BIOLOGISTS have, thanks to the magude of sampling provided by commercial ieries, a better quantitative understanding of populations with which they are concerned n do biologists interested in the quantitative ects of other marine organisms. However, iery biologists must be aware of bias that may introduced by the sampling mechanism, the ing apparatus. Fishing gear may be more ective in the capture of fish of some sizes or some areas or seasons. If the nature of the s is known allowance can be made for it, d its character may supply additional informan on the population of fish.

Longline gear, as used for tuna fishing, chareristically takes the larger tuna. It is presly used to harvest a major portion of the rld's catch of tuna, especially yellowfin tuna, *unnus albacares,* and bigeye tuna, *Thunnus esus,* from the tropical waters of the Atlantic, cific, and Indian oceans. It is apparently the ly method useful for the harvest of these ecies and, largely, of the albacore, *Thunnus lunga,* in the open ocean far from land.

The present paper is concerned with a hypoesis regarding the basis for the selection of ger fish by longline gear based on the fish nooling theory of Brock and Riffenburgh 960), together with a discussion of the relaonship between availability of fish to longline ar and the age or size composition of the stock. Only the relationship between yellowfin tuna d longline gear is considered in any detail. hile the conclusions reached for this species ay be applicable to others, there are certain ficulties involved in further comparisons. The k of any substantial surface fishery for bige tuna makes any comparisons of the character the catches between fishing methods difficult r this species. Albacore seem to be differentially distributed by size, and skipjack (*Katsuwonus pelamis*) are taken too infrequently by longline to provide useable data. Skipjack catches by longline are possibly analogous to catches of small yellowfin by the same gear.

Bluefin tuna (*Thunnus thynnus*) has not been considered; the occurrence of this species in temperate waters, subject to a variety of changes in the depth of the mixed layer, and its ability to live in both tropical and temperate marine environments, complicate any analysis. Schooling of large bluefin tuna may occur primarily for reproductive purposes.

ACKNOWLEDGMENTS

I wish to thank Mrs. M. L. Godfrey and other staff members of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, who made a special effort in organizing IBM cards containing data on longline catches for machine computation, and Dr. R. H. Riffenburgh, who supervised the programming of a computer and made the tests of the significance of the differences in lengths of yellowfin taken solitarily, in pairs, or in runs of higher numbers.

DESCRIPTION OF LONGLINE GEAR

Longline gear is a floating or drifting fishing device which takes fish by hooking and is made up of a horizontal line, to which are attached droppers ending in baited hooks. While there are modifications of the basic plan, these are not important in terms of the present analysis. Shomura and Murphy (1955) described one of the gear designs employed by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, as follows:

One unit of gear, called a basket, has 1,260 feet of mainline and six 88-foot branch lines (droppers) attached to the mainline at 30-fathom intervals. Several baskets are joined to make up

[1] U. S. Bureau of Commercial Fisheries, Honolulu, awaii. Manuscript received May 12, 1961.
Now, Biological Laboratory, Washington, D. C.

a set, the entire set being buoyed with floats at basket junctures and at the ends. Fishing at subsurface levels is accomplished by using 10-fathom lines between mainlines and floats and by setting the mainline slack so that it will sag in the water. To this end, the 1,260 feet of mainline is set in about 900 linear feet.

With this gear the minimum fishing depth is 148 feet and, of course, the droppers midway along the mainline between the floats would settle much deeper than this.

SIZE CHARACTERISTICS OF YELLOWFIN TUNA TAKEN BY LONGLINE, PURSE SEINE, AND LIVE-BAIT FISHING

Yellowfin tuna taken in the central Pacific by longline gear (Fig. 1*a*) were caught during the course of experimental and exploratory fishing by the Bureau of Commercial Fisheries. While the lengths range from 40 to 175 cm., the bulk of the fish exceed 120 cm. Figure 1*b* shows a percentage length frequency distribution of yellowfin tuna landed from the eastern Pacific (Hennemuth, 1961: table 1) by live-bait and purse seine fishing. While the lower length limit is about the same for both distributions, the largest sizes taken only infrequently by live-bait and purse seine fishing are about the same as the modal size taken by longline gear.

These distributions of lengths of fish taken by purse seine and live-bait fishing and by longline gear are typical for these fishing methods. Moore (1951) illustrates similar distributional patterns for yellowfin taken by longline and sold in the Honolulu market. Yabuta and Yukinawa (1959) give similar patterns of length distribution for fish taken in the western Pacific by this gear, as does Mimura (1958) for the Indian Ocean. Wilson and Shimada (1955) reported catches of large yellowfin by longline in the eastern Pacific; Mais and Jow (1960) reported on additional experimental longline fishing trials in the eastern Pacific, which also took large tuna, although not as large as those reported by Wilson and Shimada.

While purse seining for yellowfin tuna is largely confined to the eastern Pacific, a small live-bait tuna fishery for yellowfin off Japan takes fish of the sizes characteristic for this fishing method in the eastern Pacific (Yabuta and Yukinawa, 1957), and, from my observations occasional catches taken by this method in Ha waii are composed of small and medium siz fish.

POSSIBLE FACTORS AFFECTING SIZE OF YELLOWFIN TAKEN BY VARIOUS TYPES OF FISHING GEAR

Successful purse seine and live-bait fishing de pend upon fish being in schools, and ordinaril upon their being evident on the surface of th water. Schooling fish may not be essential fo successful longline fishing; in any event, th gear is ordinarily set without any surface ev dence of fish.

The pattern of length distribution found i the purse seine and live-bait fishing catch coul be attributed to selection against the smalle sizes (< 50 cm.) by the fishermen and to de creasing abundance of the larger sizes throug the effects of both fishing and natural mortalit Comparing length distribution of the centra Pacific longline catch with that of the easter Pacific surface fishery suggests that the forme fishing method may be ineffectual for smalle fish. However, there exists a difference in th fishing grounds which may reflect some diffe ences in population structure. In addition, th longline gear fishes at some depth; the othe two methods depend upon schooling fish locate by signs evident at the surface of the sea. Th fish available to longline gear are called th "deep swimming tunas" in fisheries literatur (Murphy and Shomura, 1955); they are pre sumed to be large in contrast to the smalle surface-dwelling fish.

Brock (1959) pointed out that areas whic sustained large surface yellowfin tuna fisheri were located on the eastern margins of the tro ical Atlantic and Pacific oceans, where the mixe or surface isothermal layer was relatively shoa For the central and western Atlantic and Pacif and all of the Indian Ocean, where the mixe layer is fairly deep, only longline gear seeme to be effective.

Both purse seine and live-bait fishing depen on surface evidence of schooling fish. Whe the isothermal surface layer is deep, schools ma appear at the surface less frequently, thus re ducing the effectiveness of these methods. Add

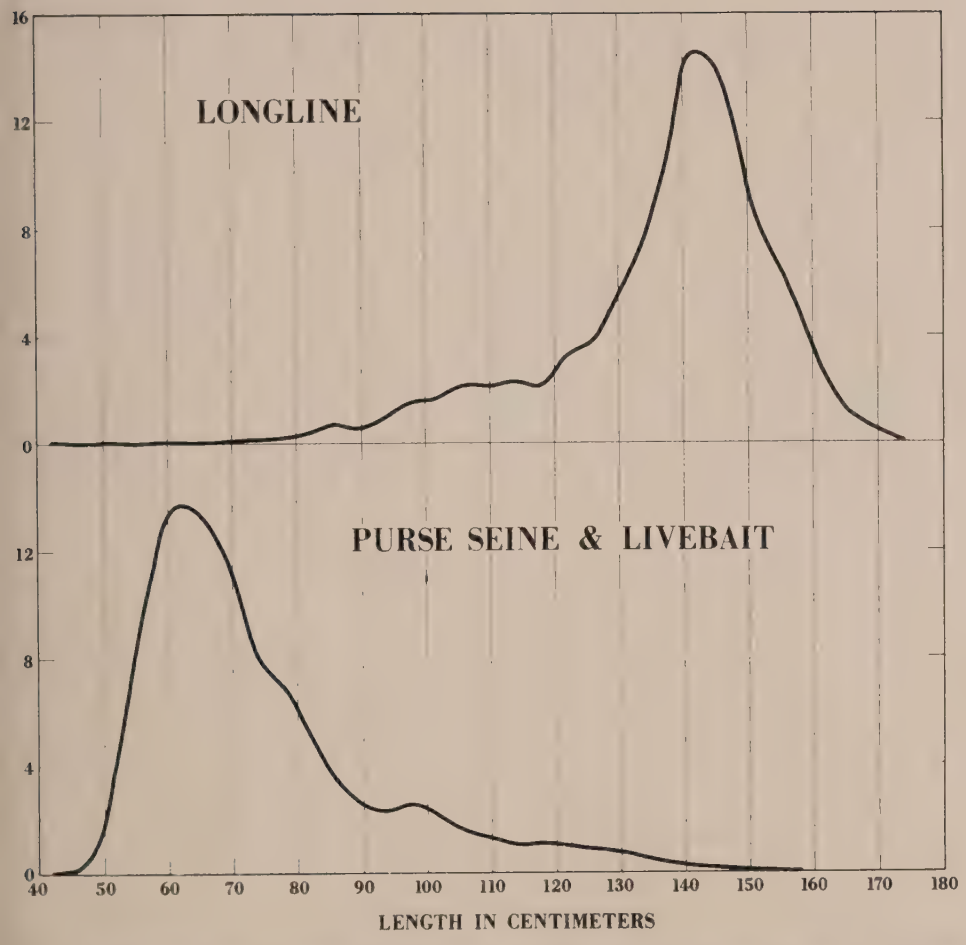

Fig. 1. *a*. Percentage length frequency distribution of yellowfin tuna taken by longline gear in the equatorial central Pacific. *b*. Percentage length frequency distribution of yellowfin tuna taken by both live-bait and purse seine fishing in the eastern tropical Pacific.

onally, if larger fish tend to form smaller hools, or no schools at all for the largest sizes, e failure of fishing methods dependent on hooled fish to take larger sizes would follow. onversely, longline gear should be most effecve for scattered fish for reasons which will be ven.

It may be pertinent, at this juncture, to dee a fish school. A number of definitions have een suggested, which are discussed in detail Breder (1959). A rather simple definition ill suffice here. A school is two or more fish the same species which respond to the others by swimming as a group. The response is assumed to be effected by vision; hence, the distance among fish within a school is less than the visual range, usually much less.

FISH SCHOOLING AND THE SIZE SELECTIVITY OF LONGLINE GEAR

If it is assumed that the number of fish in an average school is some inverse function of fish size, the low proportion of small yellowfin tuna in longline catches would be an expected consequence if longline gear was less effective

in catching fish which were schooled than those which were not. Brock and Riffenburgh (1960) show that the anticipated encounter ratio of a predator for schooled or scattered prey of some number is

$$N_e = \frac{r^3 N_f}{\left[r + c \sqrt[3]{\frac{3 N_f}{4 \pi}} \right]^3} \qquad (1)$$

where r is the visual range of the predator, N_f the number of prey, and c the average distance among individual fish in a school of N_f prey.

Equation (1) expresses the ratio of the visual densities of scattered and schooled fish. It would also express the ratio of encounter by scattered or schooled predators with some fixed number of prey, where N_f is the number of such predators and c the average distance among fish a school of predators.

It contains three variables: (1) the visu range, which is a function of water clarity; (2 the number of schooled and scattered fish; (3 the space occupied by each fish in the scho If the visual range substantially exceeds t distance among fish in a school, then a scho will scout through a substantially smaller volur of water than will an equal number of scatter fish, because the visual ranges of a large part the schooled fishes overlap; this is not true f the scattered ones. For large schools, in cle water, the encounter ratios may range from hu dreds to thousands in favor of the scattered fis These relationships are illustrated in Figur 2 and 3.

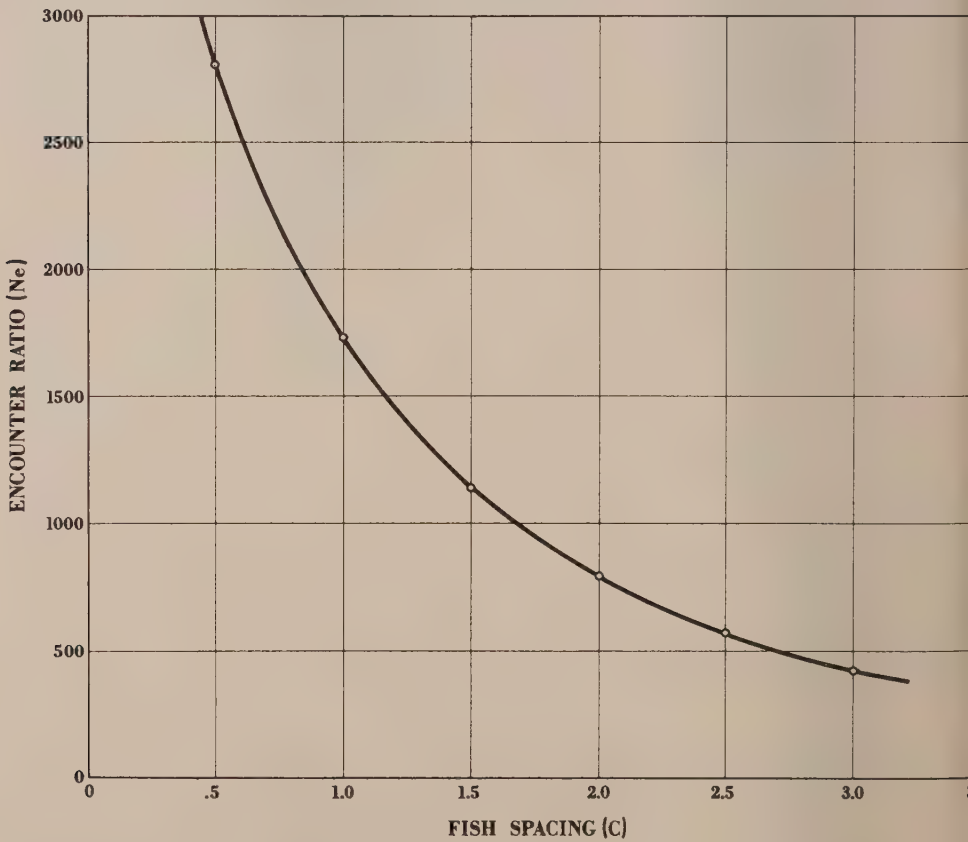

FIG. 2. Effect of increase in distance between fish in a school on the encounter ratio.

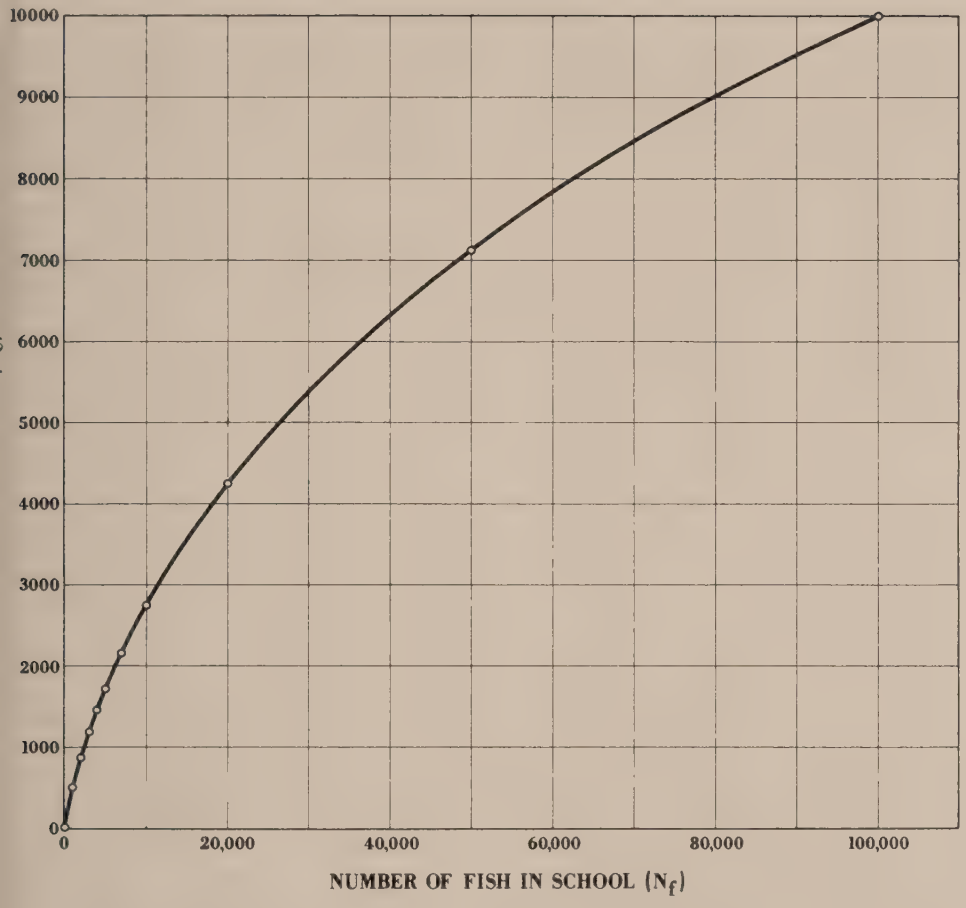

FIG. 3. Effect of increase in the number of fish in a school on the encounter ratio.

Figure 2 is a plot of the ratio N_e, the encounter ratio, against c, the distance among fish the school. Visual range is assumed to be 25 eters and school size is taken at 5,000 fish. ne increase of the encounter ratio with a reuction in the spacing (c) among fish in a hool—as compared to an equal number of attered fish—is apparent. This is to be exected, for the fish in a school approach the ndition of scattered fish as a limit as the acing among the schooled fish approaches the sual range. At this point, by definition, the hool ceases to exist. If the spacing among hooled fish were a function of fish length, the lationship shown by the figure would suggest that schooling may be less effective for large fish than for smaller ones.

Figure 3 illustrates the effect on the encounter ratio of an increase in the number of fish in a school, assuming r equals 25 meters and c equals 1 meter. The encounter ratio is, of course, determined by the particular values assigned to r, c, and N_f, if the relationship postulated in equation (1) is valid. While the values selected are arbitrary, they are not unreasonable, except possibly in the magnitude of some of the bigger schools.

A school will scout a larger volume than that scouted by an individual fish, but less than that scouted by an equal number of scattered fish.

However, on the occasion of a school encountering a set of longline gear, a probability exists that if one fish should be captured from the school, additional fish will be captured thereafter. If the movement of the school is random and confined within a given depth, a likely situation in the tropics due to the rapid cooling of water with depth below the thermocline, the probability of hooking additional fish from the school may be roughly estimated in the following way.

If a fish should be taken on the jth hook of a set of longline gear, for the ith hook there will be a component of P of the form

$$P = \frac{\pi (r+r')^2 h_{11-j1} K}{\pi (h_{11-j1})^2 d}$$

and, summing for all i hooks and simplifying, we obtain

$$\sum_{i=1}^{n} P = \frac{(r+r')^2 K}{d} \sum_{i=1}^{n} \frac{1}{h_{11-j1}} \qquad (2)$$

where h_i is the distance from the first hook taken to successive hooks (h_1, h_2, $h_3 \ldots h_n$), d the depth of water in which the fish may be expected to range, r the visual range, r′ the radius of the school, and K a factor with values between zero and one expressing the likelihood of a fish biting a baited hook.[2] An estimate of the probability of taking at least one additional fish was computed on the basis of a school of 2,000 fish with the values for equation (2) used in Figure 2, and a K value of one, a hook spacing of 54.86 meters (30 fathoms), and an isothermal layer, in which the fish occurred, 150 meters thick.

P = .7382 for 18 hooks, which would imply that additional fish may be hooked in three out of four sets of the gear where a school of the dimensions assumed here encounters a set of this number of hooks. Considering the possible high values of N_e, additional fish taken from schools may have relatively little effect toward increasing the catch from schooled as compared to scattered fish; from a school of 2,000, some 884 fish would have to be taken to cancel t effect of schooling on the basis of the sch dimensions and visual range assumed in t example. Models with increased spacing amo the schooled fish or with reduced visual rang would reduce the effect of schooling; the sumed visual range is conservative for the are where longline fishing is done. The examp does imply, however, that runs of fish may expected occasionally when a school encounte a set of longline gear, and that is the reason f presenting it.

It has been suggested that the number of fi in a school may be, on the average, an inver function of the size of fish, with the largest fi occurring either in very small schools or n schooled at all. Accepting this assumption, has been further hypothesized that the fishi efficiency of longline gear would be inverse related to the degree of schooling. If these a both true, then the longline catch should composed of a disproportionate number of no schooled fish or of fish from small schools. Ho ever, a probability exists for the capture several fish from a school, and it is reasonable assume that this probability is some function school size.

If both the assumptions and the reasoni based on them are valid, it then follows that t mean size of fish taken by longline gear occu ring in pairs or in larger groups on adjace hooks should be less than that of the solita hooked fish, and the greater the number of fi in a group the less their average size.

If such a size difference between grouped a solitary fish on longline gear does not exist, the aside from the possibility of some artifact the data, the hypothesis erected in this pap and briefly summarized above should be r jected. On the other hand, the existence of su a size difference would constitute evidence the validity of the hypothesis, lacking alte nate possible causes for this difference. It wou also, thereby, constitute evidence for the vali ity of the fish schooling theory of Brock a Riffenburgh, since a pattern of size differenc of this kind for longline gear is predicted by t theory.

Longline catch data obtained by the Bure of Commercial Fisheries in the central Paci

[2] In the case where $(r+r')^2 > h_{11-j1} d$, equation (2) cannot be interpreted as a simple probability.

the past several years were examined for dence of a difference in the size of fish taken adjacent hooks as compared to those not so en. The results are given in Table 1.

The significance of the mean difference in gth between solitarily hooked fish and all the hooked may be estimated by the Bienaymé-bycheff Inequality. While the use of this in-ality does not require any assumption of rmality of the distribution of fish lengths, it es assume that the mean and the variance of population are known. Since the sample is ge (4135), it was assumed that the mean d the variance of all fish measured would equately approximate those of the population.

$$\Pr[|\bar{x}-\mu|>e] \leq \frac{\sigma^2}{Ne^2} \qquad (3)$$

the probability of deciding that $\bar{x}$ is different m μ when it is in fact not so should be taken be 0.01, then

$$\frac{\sigma^2}{Ne^2} = \frac{389.52}{3192e^2} = 0.01, \text{ from which}$$

$$e = 3.49$$

For these data, $\bar{x} = 138.1$ and substituting s in the left side of (3), we have: $\bar{x} - 130.7 = > 3.49$.

The probability given in (3) is seen to be s than 0.01; hence the difference between the itary fish and all fish is significant.

If an assumption of normality of the distribu-ns of fish length for each of the four groups made, both the analysis of variance and the est indicate a highly significant difference ong the groups.

The assumption that runs or pairs were in-variably associated with catches from schools and that solitary fish taken were not from schools is obviously not completely true; pairs or groupings of higher numbers can occur by chance and it is at least possible to catch only a single fish from a school. The effect of chance groups and of the capture of single fish from a school would be to reduce the differences in size between the solitary fish and pairs or runs of higher numbers.

Through the application of simple probabilities, the number of fish that might be expected to be hooked in groups or individually was computed on the basis of the following assumptions.

1. The fish were randomly distributed and not schooled.
2. Fish were not caught simultaneously.
3. The catch rate was uniform at 6 fish per 100 hooks, which is a higher average rate than that for the catches in Table 1, and the gear set had 100 hooks.
4. Only a single species, yellowfin tuna, was considered in the computation, because the inclusion of other species would reduce the number of pairs and larger groups as compared to solitary fish.
5. While the end hooks on the set of gear were regarded as being available for fish, the computation of groups based on their occupancy was not made; this would also reduce the proportion of groups as compared to solitary fish.
6. The likelihood of a fish taking a hook was assumed to be the same for all unoccupied hooks.

Obviously the first fish hooked is solitary; the next fish may make a pair by taking a hook on

TABLE 1

MEAN SIZE AND NUMBER OF FISH HOOKED SEPARATELY OR IN GROUPS ON LONGLINE GEAR

NO. YELLOWFIN HOOKED SEPARATELY OR ON ADJACENT HOOKS	SAMPLE SIZE	MEAN WEIGHT (pounds)	MEAN LENGTH (centimeters)	VARIANCE (length)
1	3197	113	138.1	411.70
2	712	102	133.6	363.87
3	169	86	126.4	346.49
4	57	83	124.7	443.48
	4135			

TABLE 2

COMPUTED DISTRIBUTION OF FISH HOOKED FROM RANDOMLY SCATTERED INDIVIDUALS AND AN OBSERVED DISTRIBUTION OF THE FISH HOOKED ON LONGLINE GEAR

NO. YELLOWFIN ON ADJACENT HOOKS	SAMPLE SIZE		DIFFERENCE BETWEEN COMPUTED AND OBSERV
	Computed	Observed	
1	3919	3197	—722
2	125	712	587
3	58	169	111
4 and over	33	57	24
	4135	4135	

either side of the first fish or may take another hook elsewhere.

For each additional fish caught there are certain limited numbers of possibilities of forming pairs or larger groups. Some of these are mutually exclusive, depending upon the particular arrangement of hooked fish at that time; and the sum of the probabilities for each of these, together with the probability of taking a hook apart from those with fish, must equal one. However, by setting up all possible combinations until six fish were caught, the basis for the distribution given in Table 2 was computed. It is obvious that—on the assumption that the fish were all taken from a randomly distributed population—the agreement is very poor between the numbers of fish hooked solitarily or in groups and the numbers of fish actually caught solitarily or in groups.[3]

The comparison given in Table 2 would imply that fish in groups occurred more frequently than would be anticipated if the distribution of the fish was random. It would strengthen the inference that many of the fish taken in groups were from schools. This is in agreement with the conclusions of Murphy and Elliot (1954), who, by the examination of the frequency of "runs," found some evidence for schooling in yellowfin catches taken by longline gear.

While the comparison given in Table 2 may provide some measure of the proportion of solitary fish occurring in groups, and hence an estimate of the contamination of groups form by schools by adjacent fortuitous captures solitary fish, the information is not adequate provide a basis for adjusting the mean leng of each of the groups; the reverse contaminat of the solitary fish category by captures of sin fish from schools has not been estimated. I see no practical way of making such an estim

[3] The lack of agreement is sufficient between the "computed" and the "observed" to justify the assumption of a significant difference here without a formal statistical test.

DISCUSSION

The mechanism of size selection of yellow taken by longline gear suggested here, that schooling by fish size, if valid, has some inter ing implications in regard to the magnitude yields that may be anticipated at various fish intensities. The availability of fish for a longl fishery may, on this basis, depend primarily up the magnitude of that fraction of the popu tion which is not schooled or is in small scho In contrast, the efficiency of some other fish methods for tuna, such as purse seining and li bait fishing, depends primarily on the occ rence of fish in schools near the surface a larger than some minimum size. These fish methods presumably would take fish before th were available to longline gear.

The relative fraction of the population av able to the methods effective for schooling f as compared to those effective for scattered f would depend upon the pattern of growth a mortality.

Since fish are initially available to th methods effective for schools, a heavy fish mortality for schooling fish would certainly

the population available for longline fish- This situation would be true regardless of validity of the hypothesis proposed here re- ing the mechanisms of catch selection by e fishing methods.

mortality rates are uniform and high for stock being fished, a high catch rate by long- gear suggests that fish of schooling sizes be abundant enough to afford greater yields than those obtainable by longline fishing. This would be less true if mortality rates were much lower, especially for the medium-sized, rapidly growing fish than for the oldest fish.

To illustrate the relationship between long- line catch and the population of fish whence the catch came, the distribution of the weight of a hypothetical population in terms of age is shown in Figure 4, together with the longline

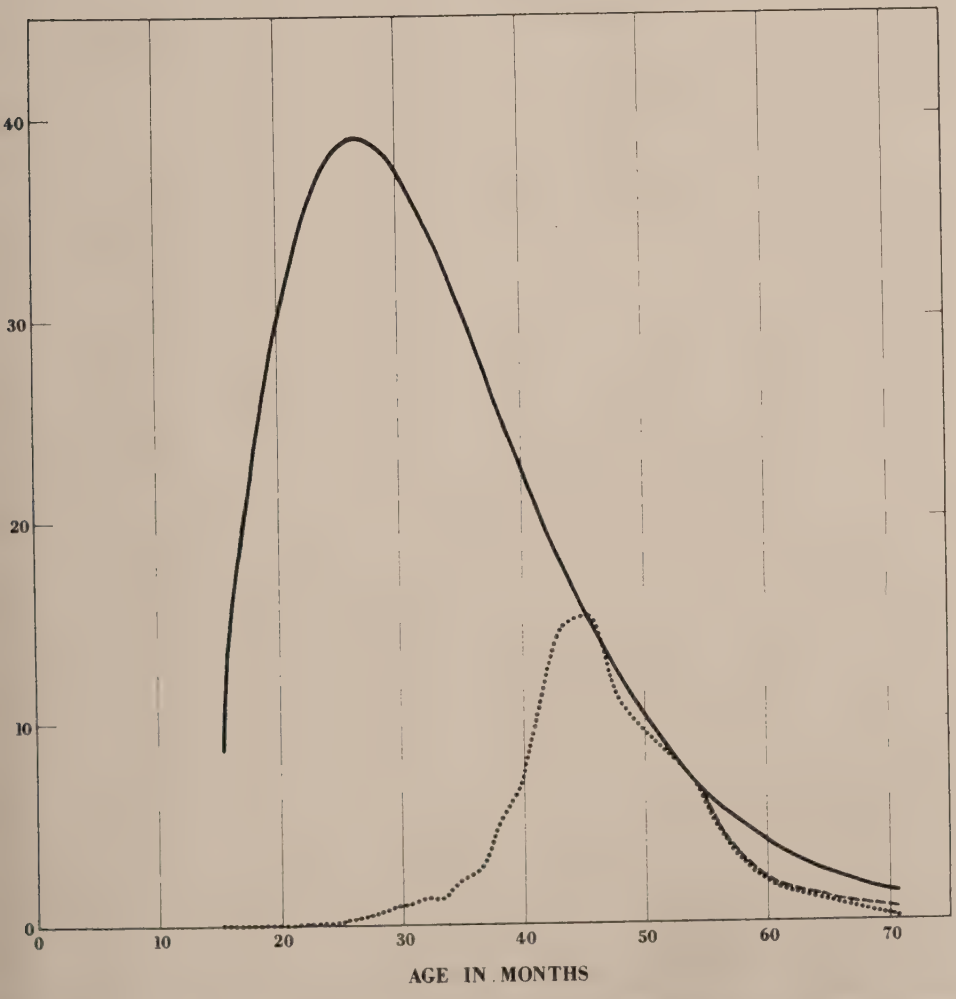

FIG. 4. Weight distribution for a hypothetical population and for fish taken by longline with identical ortality rates. The hypothetical population is shown by the solid line and by the dashed line (which is ex- ained in the text). The dotted line is the age-weight distribution of yellowfin taken by longline gear in the ntral Pacific.

catch data shown in Figure 1*a*, also transformed into a plot of weight against age.

The weight–age relationship of the hypothetical population was computed as follows:

The longline catch data depicted in Figure 1*a* were transformed into a "catch curve" by converting length classes into age classes and plotting the age frequency curve on a semi-logarithmic basis.

The transformation of length into ages was done by using the von Bertalanffy equation of growth in the form

$$t = t_o - \frac{1}{k} \ln \left(1 - \frac{L_t}{L_{oo}}\right)$$

where t is the age at length L_t, K a constant, and t_o a time constant. The values for K, L_{oo}, and t_o were estimated from the growth rates for yellowfin tuna given by Moore (1951).

Four of the age classes following the modal class approximated a straight line, the slope of which was taken as an estimate of the mortality rate of the exploited stock. The terminal age classes did not fit this line. Current work on the growth of bigeye tuna by Richard Shomura (personal communication) suggests that for this species a differential mortality by sex may occur for the largest sizes, with the females dying before the males. Assuming a differential mortality rate by sex for the largest yellowfin, an adjusted fit was made for the last four age classes on the basis that (1) the sex ratio was initially 1:1, (2) that half the remaining female fish died between ages of 54.15 months and 56.6 months, (3) that all were dead thereafter. This adjusted fit is shown as a dashed line in Figure 4. The fit is surprisingly good. The weight of fish in each age class was obtained from the length-weight relationship

$$\text{Log weight} = -7.3548 + 2.9959 \text{ Log Length}$$

where length is in millimeters and weight is in pounds. Fish approximately 15 months of age and older were included in the hypothetical population.

This estimate of instantaneous mortality for the longline catch was $e^{-1.404}$, equivalent to an annual rate of .754.

The area of the longline catch curve is about 21 percent of that for the hypothetical popul tion; this figure is an estimate of the fraction the population available to longline gear. At annual mortality rate of .374 the mode of t longline weight distribution and that for t hypothetical population would be in appro mate coincidence.

I have no means of estimating the degree agreement between the population of fish fro which the longline catches were taken and t hypothetical population depicted in Figure 4. the agreement is good, this is likely to be fo tuitous; data for longline catches are taken fro survey fishing efforts for a span of years and ov a large area of the equatorial Pacific south Hawaii. They are those catches for which bo the size and specific hook position on the set gear were recorded for each tuna taken. In add tion, the assumptions of uniform recruitme a uniform mortality rate, the growth rate us here, and equal availability of the four a classes older than the modal age class, wou have to be satisfied to obtain a good agreeme

However, the pattern of weight increase wi age is such as to suggest that longline gear, sele tively taking the largest fish, would be an i efficient harvesting method except for tu stocks subject to modest rates of mortality. may also be difficult to realize yields approac ing the maximum sustainable yield for stocks yellowfin tuna by longline gear, since increas in the catch of fish would increase mortali rates with a disproportionate reduction in cat rates. If the weight of the landings is propo tional to the weight of fish of the sizes availab to longline gear, the effect in changes in mo tality rates on catch rates may follow a patte like that given in Table 3.

The values of Table 3 are based on the grow

TABLE 3

CHANGES IN AVAILABILITY OF FISH TO LONGLIN GEAR WITH CHANGES IN MORTALITY RATES

MORTALITY RATE %	CATCH RATE %
45	100
60	37.7
75	7.2

s for Hawaiian yellowfin tuna (Moore, 1951) the pattern of size selection of fish by long- gear for the catches shown in Figure 1*a*.

he purse seine method for fishing tuna is dly developing at the present time, a situa- which may lead to the development of itable fisheries in areas where this gear is presently used. It may be suggested, how-, that for those portions of the ocean where isothermal layer is usually deep, there is now available any fishing gear suitable for oling fish when the fish may not ordinarily t the surface of the sea. This may apply with ter force to the bigeye tuna, which is only sionally caught at the surface anywhere.

SUMMARY

he selective capture of large fish by longline is described and various causes for this are ussed. One cause suggested is that small a are more highly schooled than large ones according to the schooling theory of Brock Riffenburgh, the likelihood of capture on a gline would be greatest for scattered fish.

he probability of taking more than one fish n a school on longline gear after the school ounters the longline is shown to be good, ending upon the diameter of the school and visual range of the fish.

there is an inverse relationship between the size and the number of fish in a school and ne probability of a number of fish occurring adjacent hooks is proportional to the size of school, then the mean size of the fish hooked group should be inversely proportional to number of fish in the group. This is shown oe true for longline catches made by the nolulu Laboratory in the central Pacific.

he relatively low availability of schooled to longline gear is discussed, together with probable effect of high mortality rates on the gline catch rates.

is suggested that there are no fishing meth- effective for schooling yellowfin where the ools are not present at or near the surface of sea, and that schools are apparently uncom- n in surface waters for the greater portion of the tropical Atlantic and Pacific and for all of the Indian Ocean, where the isothermal layer is deep. The possibility of an analogous situation for bigeye tuna is suggested for all tropical oceans.

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8. OPERATIONAL ASPECTS OF OCEANOGRAPHIC INSTRUMENTATION

PART III. FOR THE BUREAU OF COMMERCIAL FISHERIES (BIOLOGICAL)

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The instrumentation requirements for the investigation and charting of the biological parameters are less easily defined than the physical and chemical ones. The measurement of biological parameters are of lower accuracy and the things measured are frequently complex, making measurements difficult to compare and to define accurately.

The measurements that physical and chemical oceanographers take have value for their own sake; these measurements can be employed very usefully without reference to the biological parameters. Measurements of biological features are of less value and are more difficult to interpret if taken alone; they are most useful when they are taken in conjunction with physical measurements.

Biological measurements should be quantitative and reproduceable. It should be possible to define precisely the quantity measured. This is easier said than done. In figure 8.3 was a PLANKTON SAMPLER, a device to collect organisms from the sea. This was a towed conical net. The catch of organisms can be estimated in a variety of ways, such as by volume, weight, or species composition. However, the character and volume of catch may be different in various places and it is often quite a problem to determine what these differences reallv mean. The problem of the qualitative differences may be attacked by considering perhaps the quantity of bound nitrogen in the catch as a measure of protein, but even here the differences in average sizes of the organisms in various parts of the ocean may occasionally introduce an unknown error in the results. In addition, even the simple matter of estimating how big a change in the catch can be considered as representing a significant change in the density of organisms in

the sea itself has not been satisfactorily solved. This is essentially a sampling problem and is inherent in all observational data. These problems are not restricted to survey observations, but are of greater concern in surveys since the comparability of data taken by standardized procedures over the oceans of the earth is an important goal.

Oceanographic instruments can be grouped into two general categories: Sensing instruments and capturing instruments. SENSING INSTRUMENTS are used to obtain measurements by light or sound or some other attribute of the thing measured; a CAPTURING INSTRUMENT is used to capture the thing to be measured, and the measuring generally follows capture.

Examples of visual sensing systems are submerged automatic photographic or television cameras. Variations in the light absorption of the water itself has biological connotation, especially when taken well off shore on the high seas. Also, such a simple thing as an experienced man with a good pair of binoculars on his vessel's bridge sweeping the sea for evidence of surface schools of fish, can provide quantitative data. We used two divers to count fish observed along a line laid on the sea floor in Hawaii to estimate quantatively the abundance of inshore fishes by species and size. The object here was to compute the weight of the fish stocks per unit area of sea floor. This is, perhaps, a specialized technique but biologists have complicated problems, and tend to develop special ways to get the information they want.

In addition to visual sensing systems, there are sonic systems. Passive listening devices, such as the hydrophone, may be useful; active devices employ echo ranging equipment.

The other group is the capturing instruments. The simplest is the Nansen bottle or others of this type which collect a sample of water at a preselected depth. The Nansen bottle takes water for physical measurements such as temperature, or chemical measurements such as salinity or oxygen. Included with the water samples are animals or plants that happen to be in it.

Next is the plankton net which has been generally used for a long time by biologists as a standard instrument. It is generally used with a flow meter in the mouth. In some cases it is modified so that it can be opened and closed at various depths. A clever development of the plankton net is the continuous plankton recorder

which has been used for many years in Great Britain. In it, a strip of silk is pulled over an orifice through which water is passed. This silk is rolled up in a little chamber along with some formaldehyde to preserve the catch and thus provide a continuous record of the life that is captured at a given depth along the path of the vessel.

In addition to these small nets, there are the large nets such as mid-water trawls which are useful for sampling the larger animals of the open sea. There are many kinds and sizes, built for a variety of purposes. They are in active development; some may be modifications of commercial gear and others special designs. Stationary gill nets take in animals by entangling them and are quite selective. All nets are selective, in fact, which renders interpretation of results difficult.

The old-fashioned way of catching fish by a baited hook is still a method of capturing biological samples. Japanese longline gear and modifications thereof can be used to obtain quantitative estimates of the predators in the open sea. This gear is composed of a horizontal buoyed line which in commercial applications may be upwards of 60 miles in length. Baited hooks on droppers are hung from this, usually about 30 fathoms apart. This gear takes sharks, large tunas, marlins, and other sizable carnivorous fishes.

I have listed a number of means by which biological observations of the ocean may be taken. The sensing instruments are likely to prove more compatible with survey requirements in that they may permit continuous observations while underway or simultaneous observations with physical measurements while on station. Certain of the instruments that depend upon the capture of organisms require, in effect, a full scale fishing operation and would be difficult to coordinate adequately with the other aspects of a survey. This means that the equipment for measuring certain biological parameters, or certain trophic levels -- especially those at the peak of the food pyramid -- will not be included within the ordinary survey ship suit of instruments, but must be used on special vessels. The means of estimating these biological parameters are not perhaps adequately developed or standardized enough to justify their inclusion in the ocean survey suit of instruments at this time; they are better left as missions for research ships.

Ocean surveys will serve to give us maps of the seas in terms of physical, chemical, and biological parameters. The usefulness of these maps will depend in part on the kinds of parameters we measure and the accuracy of measurement. The problems of measurement are more acute for the biological parameters than for the others since some of the measurements to be taken have not yet become generally accepted or standardized. Without careful intercalibration, changes in measurement techniques will make comparisons of data taken prior to such changes difficult. Also, the problems involved in qualitative differences of some biological parameters even when measured by the same instrument have not yet been satisfactorily solved. However, in spite of such problems, the survey maps of the oceans will serve as a very useful basis of planning fisheries research programs and as a landmark in man's understanding of this planet.

EFFECT OF PESTICIDES ON OYSTERS

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ABSTRACT

The objective was to develop reliable methods for detecting harmful effects on oysters that might be caused by sub-lethal concentrations of chemical substances commonly used in pest control. Special equipment recorded simultaneously and continuously the shell movements of ten oysters exposed to low concentrations of test chemicals and ten control oysters. Percentage decrease in activity of test oysters was measured. Shell growth of one-year-old oysters was found to be a more useful index than shell movement. Thresholds for inhibition of shell growth were determined for 11 pesticides, of which all showed effect on growth after 24 hours' exposure to one part per million and three (chlordane, heptachlor and rotenone) were effective at concentrations as low as one part in 100 million.

INTRODUCTION

The continued and greatly expanding use of chemical pesticides has made it vital that their activity and eventual fate in the natural environment be better understood. In recent years, more than a billion pounds of chemicals have been used annually in forests, farms and homes in the war against arthropods, rodents, fungi, and weeds. For the most part we know the initial effects of these chemicals, what animals they kill or what plants they control. However, we know very little of their secondary effects. It is probable that many of these substances and their possibly-more-toxic oxidation products find their way into watersheds and eventually into estuaries and the coastal waters. These coastal waters provide either the temporary or permanent home for a large majority of our commercially important species of marine animals. Despite extensive research on the effects of pesticides in the aquatic environment, their role in marine waters is still virtually unknown.

The possible effect of these chemicals on oysters and other sedentary molluscs is of particular interest. Oysters are able to build up concentrations of some trace elements and compounds within their tissues several thousand times over that of the surrounding waters.

Whether the storage of such chemicals harms the oyster in some way or interferes with its growth, reproductive potential and vitality is not known. If oysters should concentrate chemical pesticides in their tissues, their suitability for human consumption would become suspect.

The oyster, in contrast to motile animals which can escape by swimming away, must submit to whatever changes take place in its environment. If changes should result from foreign chemicals in low concentrations, their specific effects might be difficult to identify. The oyster itself may be unaware of their presence. In objectionable concentrations, of course, the oyster responds by closing its valves for a more or less extended period of time and hence may avoid harm completely.

Our purpose in this investigation has been to develop reliable methods for identifying deleterious effects on oysters, C. virginica, resulting from exposure, over relatively long periods of time, to sub-lethal concentrations of chemicals used in pest control.

We are indebted to Lester W. Wolf of this laboratory for assistance in preparation of some of the figures.

METHODS

Initially, standard methods of bioassay were utilized for screening some of the more important pesticides to select those having acute effects on oysters at relatively low concentrations. Small yearling oysters were placed in 40-liter aquaria of standing water containing graduated concentrations of commercial pesticide formulations. Disposable plastic liners were used in the aquaria to avoid contamination from one series of tests to the next.

The oyster's ability to avoid the environment by closing its valves made it impracticable to establish standard lethal dose concentrations. Instead, such subjective criteria as shell gape and amount of fecal production were used to gauge the oyster's reaction.

For more critical analyses of toxic reactions in the oyster, shell movement was tested as a criterion of well-being. On the basis of past experience, it was felt that deviations from the normal patterns of activity on the part of the oyster when subjected to various pollutants could be readily detected.

The recording equipment was modified so that shell movements of twenty mature oysters could be recorded simultaneously (Fig. 1). Ten oysters were exposed to a constant flow of sea water approximating 17 liters per hour per oyster. The remaining half received the same amount of sea water plus a specified amount of chemical pollutant.

The test chemical was made up in a concentrated stock solution in acetone which, by itself, had no demonstrable effect on oysters at the concentrations used. This pesticide solution was metered into a mixing chamber by means of a calibrated stop-cock and flowed from there into the test aquarium.

Chemicals were used in as pure form as could be obtained commercially; experimental dilutions were made on the basis that they were 100 per cent pure. Some formulations contained more or less inert material and, consequently, the effective dilution in these instances was correspondingly greater.

Continuous kymograph recordings of shell movements showed when oysters were closed, or open and presumably feeding, as well as the degree of "normalcy" of the movements. It is possible to compare the degree of activity of control and experimental oysters by a simple calculation based on the number of hours each oyster was open as compared to the total number of elapsed hours.

As an additional check, containers of 30 measured spat (Fig. 1,K) were placed so as to receive the discharge from the experimental and control oyster aquaria. These spat were measured each week to determine linear growth increments.

After completion of the first series of tests, it was apparent that measured increases in spat growth provided data that were not only more critical but also easier to obtain and more susceptible to statistical analysis. Consequently, additional equipment was arranged to provide data on growth rates only (Fig. 2).

Yearling oysters, approximately 1.5 inches in length, were filed with an iron rasp so that all soft new shell growth on the valve edges was removed. Care was taken to avoid making an opening into the shell cavity. The oysters were measured to the nearest millimeter and individual records maintained. Subsequent measurements were made at regular intervals so that the daily linear increment could be identified. There was no evidence that removal of the new shell growth by filing irritated the experimental or control oysters. This technique insures that new growth will be linear and can be measured. Otherwise, some growth would be devoted to thickening of the new shell and would be difficult to assess.

Fig. 1. Equipment used to expose large oysters to a continuous flow of chemical pollutants. Insert shows model of recording arrangement. Oyster (A) is mounted on weight, a fine line fastened to upper valve with wax passes around pulleys (B, C, D), and terminates with small weight (E) which maintains tension. As pulley C is turned by shell movement, it activates capillary pen (G); ink supply is at F. The stock solution of a chemical (H) is metered into baffle and mixing chamber (I), passes into the test chamber of oysters (J), and is discharged through tray of small oysters (K). Kymograph is at L.

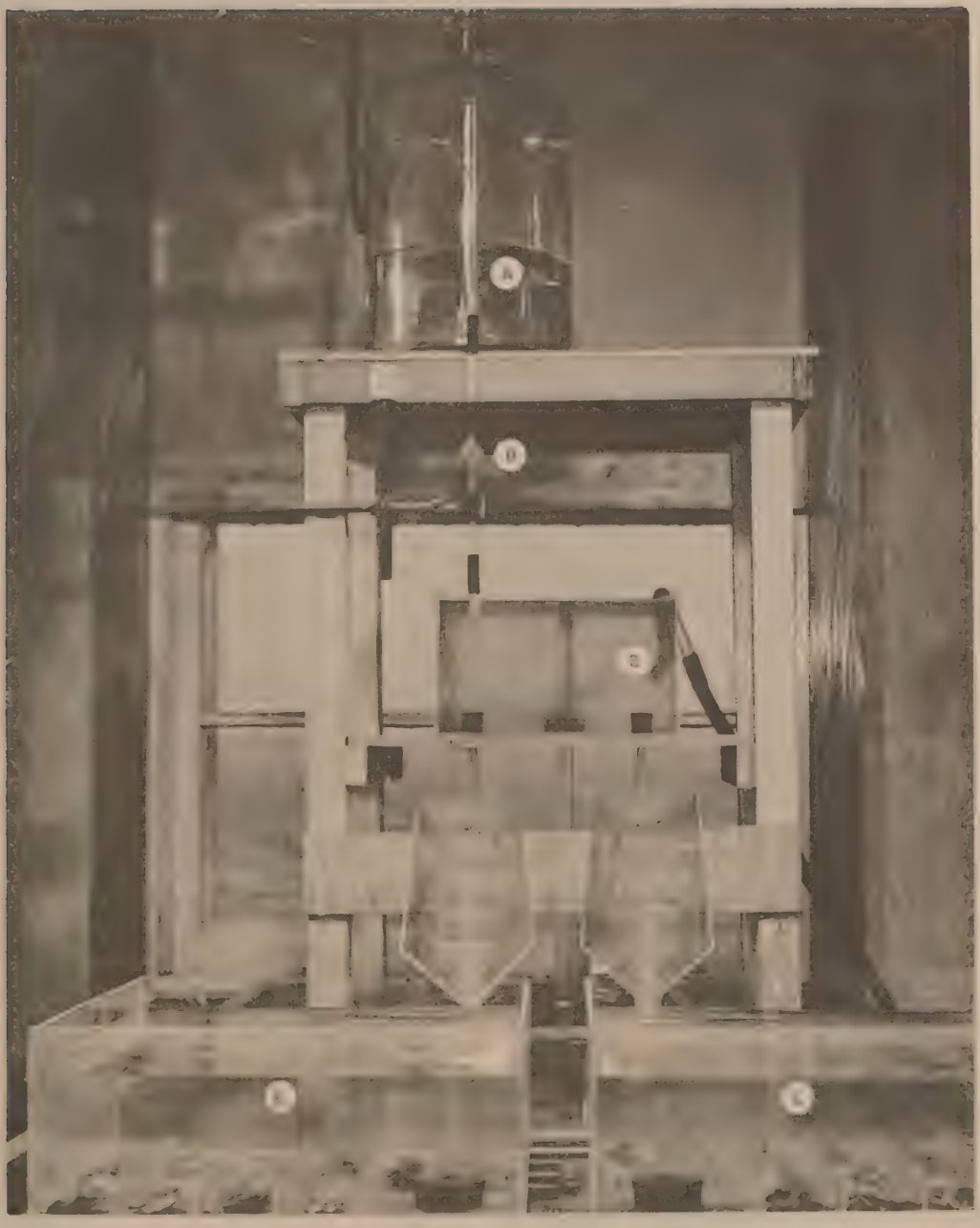

Fig. 2. Equipment used to expose small oysters to a continuous flow of chemical pollutants. Control (C) and experimental (E) aquaria are divided into compartments which do not interfere with water circulation but permit identification of fecal material produced by individual oysters. Stock solution of pollutant (A) is metered by stopcock (B) into mixing baffle. Seawater flows from constant level chamber (D) into both aquaria by ways of baffles.

Threshold toxicity concentrations were estimated by observing the reactions of twelve oysters for a day. When the working dilution was selected, fifty young oysters were used for each test in addition to an equal number of control animals. The oysters were measured at daily intervals for three to ten days depending on the degree of toxicity observed.

Early rough screening tests indicated that dieldrin and toxaphene were particularly irritating to oysters, so these chemicals were selected for our testing program to determine the suitability of these methods for identifying possible chronic toxicity at relatively low concentrations.

RESULTS AND DISCUSSION

The toxic effects of pesticides on oyster activity may be visualized by the typical kymograph records shown in Fig. 3. Tracings of shell movement of control animals are primarily horizontal lines indicating a fairly constant shell gape while the animals are pumping water and feeding. Intermittent snap closures to eject faeces are indicated by the small vertical pen marks. The record of the experimental oysters shows clearly the irregularity of the shell movements, numerous closures and slow reopenings. Obviously, these experimental animals could not have been pumping water efficiently.

Analyses of activity records of oysters subjected to toxaphene and dieldrin at a concentration of 0.1 ppm are presented in Fig. 4. The harmful effects of toxaphene (A) are clearly shown by the 70 per cent decrease in activity of experimental as compared to control oysters at the end of the fourth week when the experiment was terminated. Similar but not as severe effects were observed using dieldrin. At the end of the fifth week, experimental oysters showed only 50 per cent of the activity of control oysters.

In both experiments, trays of small oysters (K in Fig. 1) received the discharge from the experimental and control aquaria. Data on weekly growth increments of these oysters (Fig. 4) show the inhibiting effect of the pollutants clearly. For example, with toxaphene no growth occurred in the experimental group after the second week.

It is of interest that no significant changes in the activity of large oysters exposed to dieldrin could be detected for the first two weeks even though growth was inhibited in the small oysters from the start. After the fifth week of exposure to 0.1 ppm of dieldrin the results appeared to be decisive so the toxicant was discontinued. In the

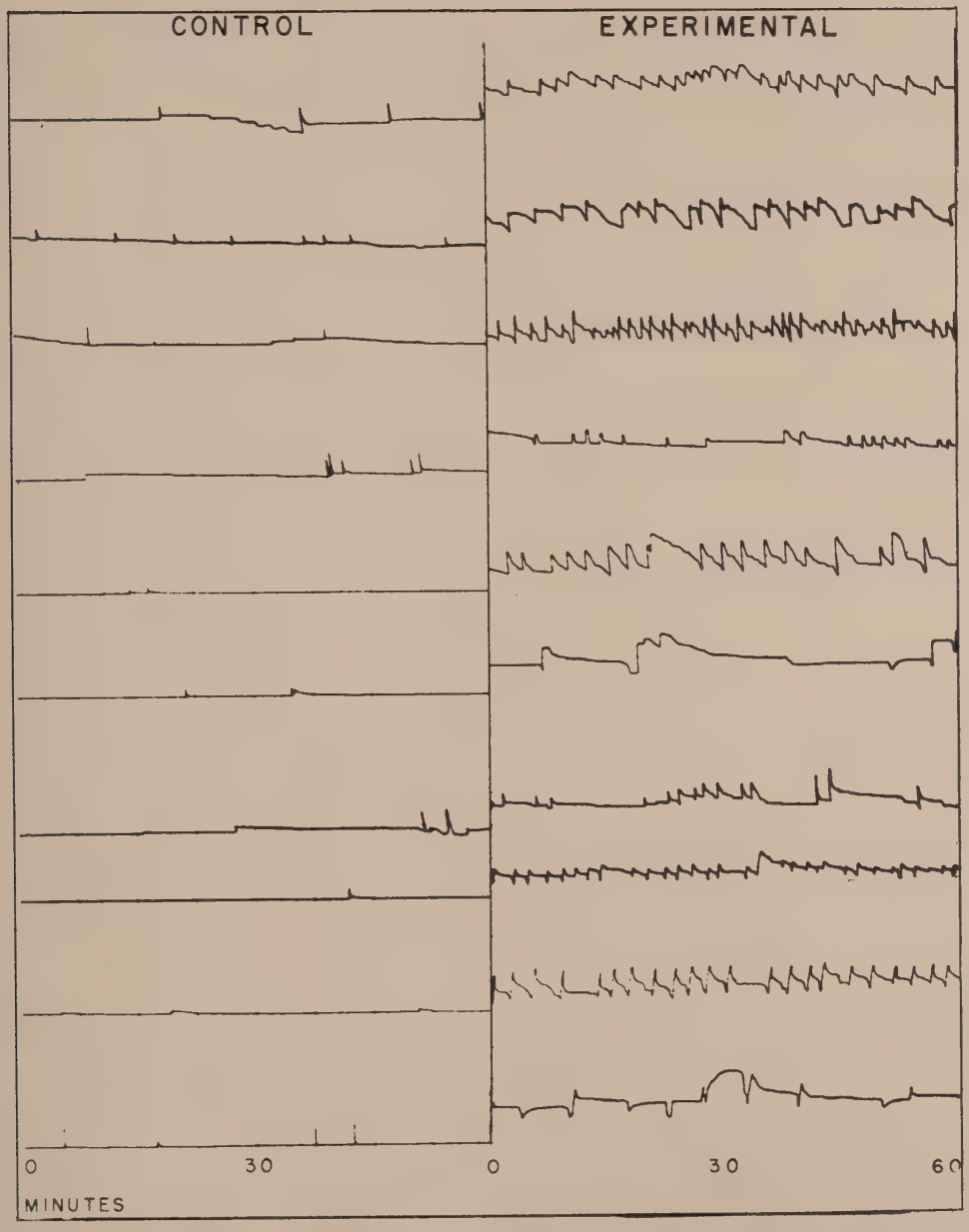

Fig. 3. Kymograph records of ten oysters prior to exposure (Control) and of the same ten oysters after ten hours of exposure to 1.0 ppm dieldrin (Experimental). Vertical tracings indicate shell closures.

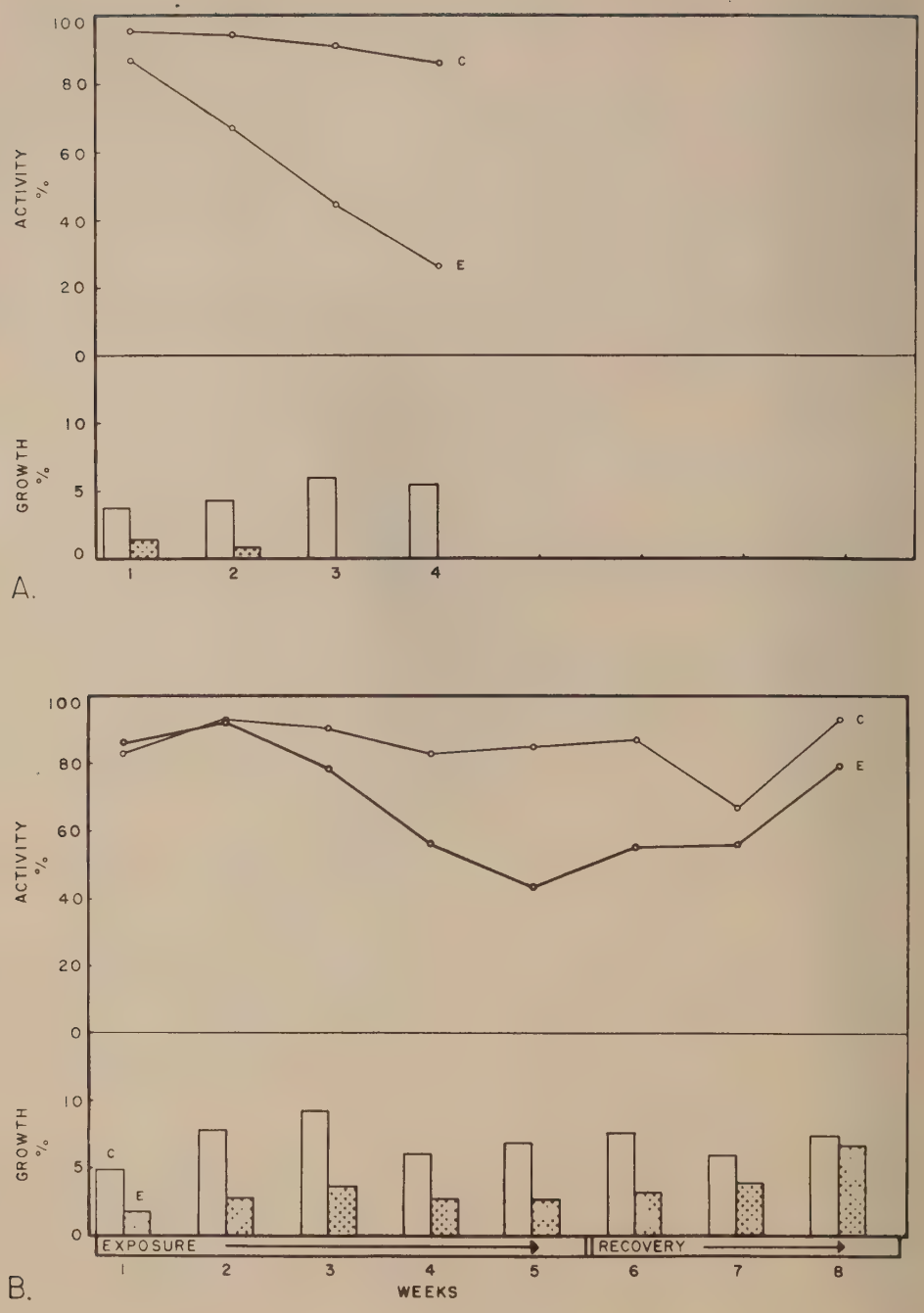

Fig. 4. Activity of large and growth of small oysters exposed continuously to (A) 0.1 ppm toxaphene and (B) 0.1 ppm dieldrin. Activity calculated as ratio of hours open to elapsed hours; growth calculated as per cent increase in length per week.

following three weeks it is apparent (Fig. 4, B) that both the activity of the large oysters and the growth rate of the small animals were returning gradually to the pattern shown by the controls throughout the test period. Whether this return to normal is characteristic of oysters exposed to other pesticides is not yet known. The graph (Fig. 4, B) depicts a sharp decrease in the activity of control oysters during the seventh week. This was correlated with a marked decrease in water temperatures for that period.

In the last series of observations, data on the growth rate of small oysters exposed to a series of chemical pesticides were collected as described earlier and shown in Fig. 2.

Table 1 lists the common pesticides tested to date which, at the indicated concentrations, affect oyster growth rates within a period of 24 hours. In all cases, growth rates were at least 35 per cent, in some cases 100 per cent, less than the control group. It is reasonable to assume that even greater dilutions might have had deleterious effects after longer periods of exposure. In all of the testing program, it was found that the first objective criterion of toxicity to appear was the decrease in shell deposition.

Table 1. Common pesticides which inhibit the growth of young oysters after 24 hours' exposure

Chemical and per cent active ingredients		Minimum effective concentration in parts per million
Aldrin	93	0.1
Chlordane	100	0.01
o-Dichlorobenzene	100	1.0
DDD	50	1.0
DDT	100	0.1
Dieldrin	100	0.1
Endrin	97	0.1
Heptachlor	74	0.01
Rotenone	98	0.01
Sevin	95+	1.0
Toxaphene	60	0.1

CONCLUSIONS

1. Yearling oysters are suitable bioassay animals for evaluating chemical pollutants in the marine environment.

2. Changes in growth rates of small oysters can be detected in one or two days but decreases in shell activity in larger oysters may not be obvious until after one or two weeks of exposure.

3. Common agricultural pesticides may inhibit the activity and growth of oysters at concentrations as low as one part in 100 million after only 24 hours of exposure.

4. There is limited evidence that these chemicals are not stored by the oyster and that recovery takes place when the pollutant is removed from the environment.

5. Each of the 11 common pesticides tested has been found toxic to oysters and would curtail growth rates severely if present in the environment at the stated minimum concentrations for an extended period.

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Western Atlantic Fishes of the Family Priacanthidae[1]

DAVID K. CALDWELL

A key, based on meristics, is presented for ıe four species of the family Priacanthidae ccurring in the western Atlantic: *Pseudo-riacanthus altus* (Gill), *Priacanthus cruen-ıtus* (Lacépède), *Priacanthus arenatus* Cuvier, and *Cookeolus boops* (Bloch and Schneider). Geographical ranges are noted and certain limited systematic and ecological comments are included.

THE fishes of the family Priacanthidae constitute a compact group of percoorph fishes which can be distinguished from ther members of the order by a reduced umber (16, the 14 innermost branched) of rincipal caudal fin rays.

Four species of Priacanthidae are presently recognized in the western Atlantic, all occurring in the continental waters of the United States. Major western Atlantic ichthyological faunal works give keys to the adults of two or three species only (see for example Jordan and Evermann, 1896; Meek and Hildebrand, 1925; Breder, 1948; Beebe and Tee-Van, 1933; Evermann and Marsh, 1902;

[1] Contribution No. 60 from the U. S. Fish and Wild-'e Service, Bureau of Commercial Fisheries, Biological aboratory, Brunswick, Georgia.

and Hildebrand and Schroeder, 1928). However, none of these works include *Cookeolus boops*. I find but one work which deals with all of the family in this region and includes a key to all of its members. This is an early paper by Morrison (1890), in which the author bases his findings on very limited material or on literature alone. While quite useful, his keys lack sufficient ranges of meristic characters. In addition, fishes of this family undergo considerable ontogenetic change, and many characters used in existing keys either do not manifest themselves in the very young, or the young of different species may have key characters in common which become differentiated in the adults.

All western Atlantic priacanthids possess 10 dorsal and three anal spines.

Pseudopriacanthus altus can be separated from the other three western Atlantic species on any one of four characters: numbers of dorsal or anal soft-rays, lateral-line scales, or vertical scale rows. A full complement of vertical fin soft-rays was established in this species by a size of 6.6 mm, lateral-line scales were certainly established by 26.4 mm, and vertical scale rows by 23.8 mm (Caldwell, *in press*). The characters in the key were established for the other species at least down to the following sizes: *Priacanthus cruentatus*, 25 mm; *Priacanthus arenatus*, 24 mm; *Cookeolus boops*, 37 mm.

Cookeolus boops further can be separated from the other three species on the basis of its unusually long pelvic fins (spine never less than 28 per cent of standard length, as opposed to never more than 27 per cent in the other three species; second soft-ray never less than 45 per cent of standard length, as opposed to never more than 43 per cent in the other species—all of these percentages decrease in larger fish). The dorsal and anal fin rays also are longer in *Cookeolus* (see Figs. 1–4).

The western Atlantic species have close relatives throughout the warm waters of the world, and it is likely that where these meristics are used in distinguishing the species they can be relied upon in specimens down to similar small sizes.

The four western Atlantic species are assigned to three genera. The proof of validity of one genus and the proper generic name for another must await clarification through work now being undertaken. It is not within the scope of this paper to anticipate the results of these studies, but the key presente herein serves also as a generic key to th family Priacanthidae in the Atlantic as th genera may presently be recognized. Ne meristic data presented in this paper a embodied in the key. For general morph logical and morphometric descriptions western Atlantic species, the reader is r ferred to Jordan and Evermann (1896), *Pri canthus* and *Pseudopriacanthus;* Morriso (1890), all species; Boulenger (1895), a species; Meek and Hildebrand (1925), *Pri canthus;* Reid (1944) and Fowler (1947 *Cookeolus*.

Methods

Measurements were made with fin pointed dial calipers in straight lines fro point to point. Meristic counts were mad under magnification. Standard length w measured from the tip of the snout (n at the midline, but at the lateral projection to the posterior end of the hypural pla (base of mid-caudal rays). Unless otherwi stated, all lengths are standard length. Th last dorsal soft-ray and anal soft-ray a split to the base and the two branches we counted as one. The penultimate soft-ra of these fins may be very close to the la soft-ray and care should be exercised making these counts. Gillraker counts we made on the first arch, usually of the righ side of the fish. Rudimentary gillraker often one or two occurring at the origin either limb, were included in the total cou for that limb. A gillraker located at th junction (angle) of the upper and lowe limbs was included in the count for the lowe limb. Only lateral-line scales with a com plete tube were counted. Sometimes th tube system extended onto an adjacent sca slightly above or below the main scale ro and this incompletely-pored scale was n counted. Judgment about the completene of a tube may distort the scale count by on or two scales. The first pored scale occu near the upper angle of the opercular ope ing, and all completely-pored scales we counted back to and including the one cove ing the junction of the mid-caudal rays an the posterior edge of the hypural comple Usually, several additional pored scales e tended onto the caudal rays, but these we not counted. In counting vertical scale ro a similar question of judgment, resultin from irregular arrangement of rows, ma

so lead to a difference of one or two rows
count. The number of these anteriorly
blique vertical rows was counted along the
idline of the body, beginning at a point
st below the anterior terminus of the
teral line (counting from and including
e first complete scale on the cleithrum)
nd continuing posteriorly to the caudal fin
se. Like the pored-scale row, several ver-
cal rows of scales continue onto the caudal
n, and the last row counted was the one
hich when visually extended anteriodorsally
cluded the last pored scale counted.

Sources of Materials

The sources of *Pseudopriacanthus altus*
ere listed previously (Caldwell, *in press*).
am indebted to the following museums and
dividuals for making material of the other
ecies available to me for study: Academy
Natural Sciences of Philadelphia (ANSP),
rough James E. Böhlke; United States
ational Museum (USNM), through Leon-
rd P. Schultz; University of Michigan Mu-
um of Zoology (UMMZ), through Reeve
. Bailey; Cornell University Museum
CU), through Edward C. Raney; Institute
Jamaica (IJ), through C. Bernard Lewis;
niversity of California at Los Angeles (W),
rough Boyd W. Walker; University of
lorida (UF), through John D. Kilby; Uni-
rsity of Georgia (UG), through Donald
. Scott; University of North Carolina Insti-
te of Fisheries (UNC), through Earl E.
eubler, Jr.; Gulf Coast Research Labora-
ry (GCRL), through Gordon Gunter;
obert H. Gibbs, Jr. (RHG); Marine
udios, Marineland, Florida, through F. G.
Vood; and U. S. Fish and Wildlife Service
hthyological Laboratory (USFWS Ich.
ab.), through Giles W. Mead.

In addition to these, numerous specimens
ere made available by Harvey R. Bullis,
r., from collections of the U. S. Fish and
Vildlife Service exploratory fishing vessels
Oregon, *Silver Bay*, and *Combat*. These are
eposited at the U. S. Fish and Wildlife
ervice Bureau of Commercial Fisheries Bio-
gical Laboratory at Brunswick, Georgia.
long with collections from the Service vessel
Theodore N. Gill (BLBG). Bullis' color
ides of a living *Priacanthus cruentatus* are
lso greatly appreciated. Materials examined
re listed under the species.

Acknowledgments.—I wish to thank my
ife, Melba C. Caldwell, for assistance in
many ways during the final stages of the
study and preparation of the manuscript.
William W. Anderson and Jack W. Gehr-
inger, both of the Brunswick laboratory,
made numerous helpful suggestions in read-
ing the manuscript. Hugh M. Fields assisted
in the early phases of the study by making
some of the measurements and counts.

1. *Pseudopriacanthus altus* (Gill), 1862:132
Fig. 1

Relationships.—Myers (1958), in pointing out an earlier paper by White (1936), proposed that the generic name *Pristigenys* Agassiz be applied to this group rather than the still-generally-accepted generic name *Pseudopriacanthus* Bleeker. *Pristigenys* is based on a fossil, and until completion of analysis of data for a world-wide revision of this genus by W. I. Follett and myself, I use the name *Pseudopriacanthus*.

Range.—Southern Gulf of Maine to Pensacola, Florida, and scattered localities (dependent on bottom type) throughout the Gulf of Mexico; Cuba; Virgin Islands; Bermuda; and possibly the Bahamas (record based on a specimen from stomach contents of a pelagic predator taken off the west end of Grand Bahama Island, possibly from nearby in the Gulf Stream). Contrary to most published ranges indicating this to be a West Indian form, this species is known from the West Indies by only five specimens, all recently captured (Caldwell, *in press*). The identity of a specimen described and figured by Miranda Ribeiro (1961:8) as *P. altus* from off southern Brazil (between Florianopolis and Laguna) is uncertain, but it is clearly not this species.

Material examined.—In a recent study of the development and distribution of this species (Caldwell, *in press*), I examined 264 specimens, ranging from 2.2 to 262 mm, from throughout the species' range. The localities for these specimens and pertinent ecological data were included in that paper.

2. *Priacanthus cruentatus* (Lacépède), 1803:522
Fig. 2

Relationships.—*P. cruentatus* usually is considered synonymous with *P. carolinus* Lesson (1826:224) of the eastern to western Pacific (see Jordan and Evermann, 1896:1238). Gillraker counts taken on specimens from the Atlantic and Pacific support this con-

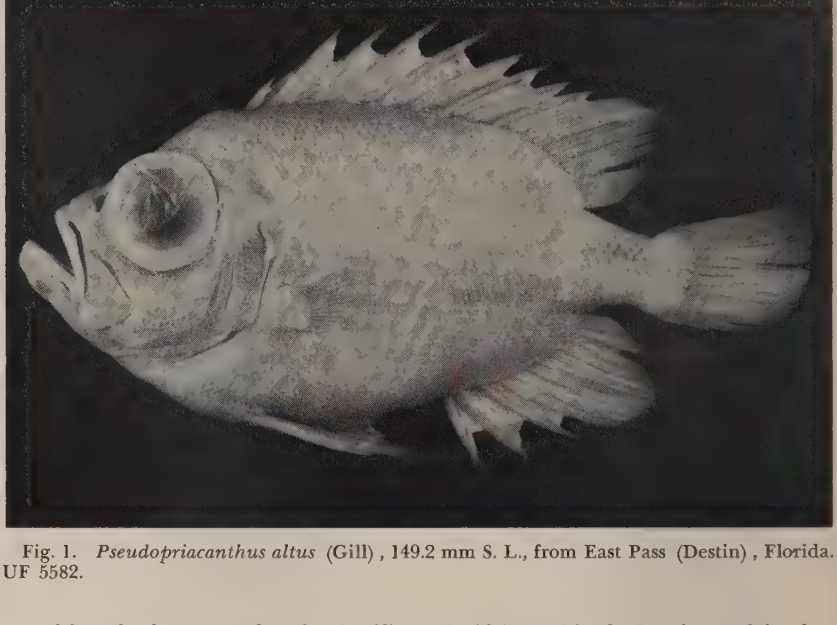

Fig. 1. *Pseudopriacanthus altus* (Gill), 149.2 mm S. L., from East Pass (Destin), Florida. UF 5582.

clusion, although the mean for the Pacific specimens was slightly higher (Table 1).

Range.—Both sides of the Atlantic and in the eastern to western Pacific. In the western Atlantic from off Cape May, New Jersey (a northward range extension from southern Florida) to Rio de Janeiro and in the Gu of Mexico.

Table 1. Comparative Counts of First-Arch Gillrakers for *Priacanthus cruentatus* from the Western Atlantic and Eastern Pacific Oceans

	Numbers of Gillrakers	Numbers of Specimens	
		Western Atlantic	Eastern Pacific
Upper limb	5	9	13
	6	—	5
Lower limb	16	1	—
	17	5	3
	18	3	6
	19	—	8
	20	—	1
Total arch	21	1	—
	22	5	2
	23	3	4
	24	—	10
	25	—	2

Material examined.—ATLANTIC—11 spe imens, ca. 25 to 185.2 mm, as follows: 38°5 N, 66°26′ W, 2 (RHG); 34°14′ N, 76°01′ W *Silver Bay* 1247, 1 (BLBG); 29°00′ N, 77°0 W, *T. N. Gill* Cr. 3 Spec. Sta. 6, 1 (BLBG) 5 mi. W Nassau, N. P., Bahamas, 1 (UF 2 (UF); Negril, Jamaica, 3 (IJ). PACIFIC 18 specimens, 71.7 to 206 mm, as follow Honolulu market, Hawaii, 2 (UMMZ 56686 Hawaii, 1 (UMMZ 60529); Hannibal Ban Panama, 07°25′ N, 82°05′ W, 1 (W 51–243) Isla Cocos, Costa Rica, 8 (W 58–378).

Live-color note.—On 23 June 1958, Jac W. Gehringer of the Bureau of Commerci Fisheries Biological Laboratory at Brunswic Ga., dipnetted a 29.1-mm specimen (BLBG of this species in the late afternoon at th surface at *Oregon* station 2198 (southweste Gulf of Mexico). From his live-color note and Kodachrome slides by Harvey R. Bull Jr., of the specimen alive in an aquarium, have prepared the following descriptio Ground color of sides and belly silver. Do sum deep blue with six distinct royal blu saddles over the back and extending abou one-third the distance down the side Lighter blue saddles between these extende only half as far down the sides. Several larg irregularly placed, dark blue spots on th

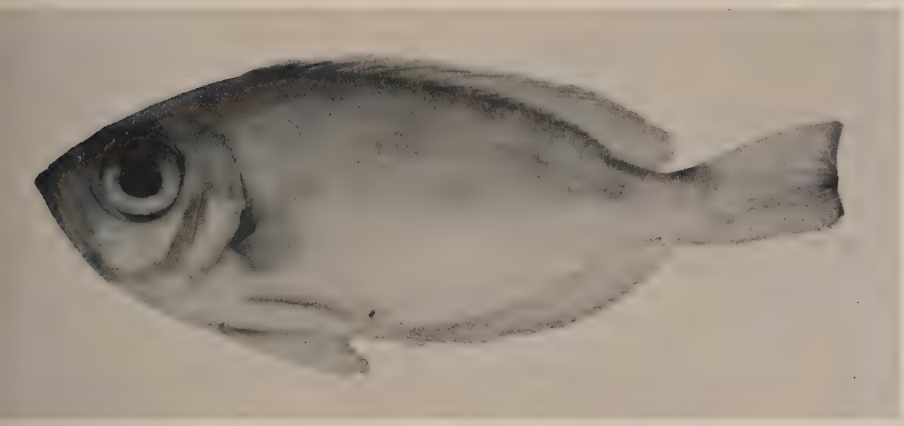

Fig. 2. *Priacanthus cruentatus* (Lacépède), 161.8 mm S. L., from 5 mi. W of Nassau, N. P., Bahamas. UF uncat.

les below the saddles. Pectoral and caudal is transparent; pelvic, dorsal, and anal fins ansparent with royal blue spots of varying es. Eye grey, mottled with silver and with black pupil. An irregular blue blotch der orbit—between it and mouth. The odachromes show a slight reddening around me of the lateral spots and saddles, and it ay take only a few hours at most at the ttom (in this case, in an aquarium) for e red coloration to be assumed (all bottom-velling individuals of this family are red). his same pattern is retained in bottom-ring specimens, with the blues represented carmine, and the silver by rose. This demonstrates that the pelagic forms *P. cruentatus* have the coloration expected r pelagic prejuveniles of species with bottom-living juvenile and adult stages (see Hubbs, 1941:184). I would expect the pelagic forms of the other three western Atlantic species to demonstrate a blue-silver coloration, and all priacanthids probably exhibit it.

3. *Priacanthus arenatus* Cuvier, 1829:101
Fig. 3

Relationships.—Possibly synonymous with forms of the Pacific and Indian oceans.

Range.—Listed by Briggs (1958:275) as: Both sides of the Atlantic; in the western Atlantic from Bermuda and Massachusetts to Argentina (35° S), and widespread in the Gulf of Mexico. I found no extensions to the range.

Fig. 3. *Priacanthus arenatus* Cuvier, 149.3 mm S. L., from 07°18′ N, 56°49′ W, *Oregon* sta. 2262. BLBG uncat.

Material examined.—67 specimens, 23.9 to 306 mm, as follows: Orient, Long I., N. Y., 1 (CU 7972); 38°58′ N, 66°26′ W, 1 (RHG); 34°39′ N, 76°27′ W, *Silver Bay* 1262, 1 (BLBG); 34°29′ N, 76°49′ W, *Silver Bay* 1305, 1 (BLBG); 32°59′ N, 78°24′ W, *Silver Bay* 1357, 1 (BLBG); 32°51′ N, 78°32′ W, *Silver Bay* 1360, 1 (BLBG); 12 mi. E of Knuckle Buoy, N. C., 1 (UNC 778); 29°58′ N, 80°32′ W, *Silver Bay* 2083, 1 (BLBG); 29°52′ N, 80°26′ W, *Silver Bay* 2144, 1 (BLBG); 29°50′ N, 80°27′ W, *Silver Bay* 2143, 2 (BLBG); 29°44′ N, 80°25′ W, *Silver Bay* 2078, 1 (BLBG); 28°08′ N, 94°35′ W, *Silver Bay* 10, 2 (GCRL); 28°20′ N, 94°97′ W, *Silver Bay* 187, 3 (USNM Acc. 225026); off St. Marys, Ga., 1 (BLBG); 25°13′ N, 80°10′ W, *Combat* 455, 1 (BLBG); off Miami, Fla., 1 (CU 26164); 25 mi. NNE of Tortugas, Fla., 2 (UG 161); off Pulaski Light, Tortugas, Fla., 3 (UG 199); 22°13′ N, 89°43′ W, *Silver Bay* 404, 1 (USFWS Ich. Lab.); 23°13′ N, 89°00′ W, *Silver Bay* 431, 2 (BLBG); 23°36′ N, 87°54′ W, *Silver Bay* 438, 1 (BLBG); "Florida," 5 (USNM 117071), 1 (USNM 117072); 26°46′ N, 96°20′ W, *Oregon* 1091, 1 (UF); 26°11′ N, 96°52′ W, *Oregon* 1082, 1 (UF); 26°10′ N, 97°00′ W, *Oregon* 1085, 1 (UF); 18°43′ N, 93°30′ W, *Oregon* 1060, 1 (UF); 20°02′ N, 91°59′ W, *Silver Bay* 359, 6 (BLBG); 20°06′ N, 91° W, *Silver Bay* 351, 5 (BLBG); 21°02′ 91°56′ W, *Silver Bay* 381, 2 (BLBG); 22° N, 90°03′ W, *Silver Bay* 398, 2 (BLBG); side of Eluthera Is., Bahamas, 1 (UF); Ped Bay, St. Elizabeth, Jamaica, 1 (IJ); 18°51′ 64°38′ W, *Oregon* 2617, 2 (BLBG); 07° N, 57°45′ W, *Oregon* 2343, 1 (BLBG 07°18′ N, 56°49′ W, *Oregon* 2262, 3 (BLBG 06°56′ N, 56°43′ W, *Oregon* 2265, 1 (BLBG Aquadilla, 1 (USNM 50138).

4. *Cookeolus boops* (Bloch and Schneider 1801:308
Fig. 4

Relationships.—This species, as well as t others of the genus, is often ascribed to t genus *Priacanthus*. Fowler (1928:190) fi described *Cookeolus* as a subgenus of *Pr canthus*, but later (1947) elevated it generic rank. The generic distinction is tained pending results of further study.

Reid (1944:216) did not believe his spe men from off Cape Henry, Virginia, was t same as *Priacanthus boops* "from Japan" a so recorded it as *Priacanthus bonarien* Cuvier (1829:105). In doing so, he disagre with Devincenzi (1924:226), who had syno ymized *P. bonariensis* with *C. boops*.

Fig. 4. *Cookeolus boops* (Bloch and Schneider), 158.4 mm S. L., from 20°52′ N, 73°41′ W, *Silver Bay* sta. 3498. Explor. Fish. and Gear Res. Sta., USFWS, Brunswick, Ga., uncat., through BLBG.

ops was not originally a Japanese species, Reid apparently believed, but was de-ibed from near St. Helena in the South lantic. All Atlantic forms are generally cognized as belonging to the one species (*C. ops*). Even in comparing my material with ecimens of the Japanese species, *C. japoni-s* Cuvier (1829:106), I was unable to see the fferences referred to by Reid; i.e., in eye ameter and preopercular-spine structure. mparison of my six western North Atlan-specimens with two from Japan revealed differences.

A specimen from off southern Brazil listed d figured by Miranda Ribeiro (1961:8) *Pseudopriacanthus altus* is clearly not is species but best fits *C. boops*, although ny pertinent facts were omitted from his scription. His specimen reportedly has dorsal soft-rays and 13 anal soft-rays.

Range.—Both sides of the Atlantic and ssibly throughout much of the Pacific. the western Atlantic from off Cape May, J., to Buenos Aires, Argentina.

Material examined.—*Cookeolus boops*—6 ecimens, about 37 to 220 mm, as follows: 40 mi. SE of Five-Fathom Bank, off Cape ay, N. J., 1 (ANSP 72102), 1 (ANSP 099); 80 mi. SE of Cape Henry, Va., 1 JSNM 120996); 36°57′ N, 68°05′ W, 1 RHG); 20°52′ N, 73°41′ W, 1 (Explor. sh. and Gear Res. Sta., USFWS, Bruns-ck, Ga., through BLBG); Havana, Cuba, (UMMZ 171872). *C. japonicus*—2 speci-ens, 105.6 and 114.5 mm, as follows: isaki, Japan, 1 (CU 33314), 1 (UMMZ 2693).

Ecological note.—Like those of *Pseudopria-nthus* and *Priacanthus* (see Caldwell, *in ess*), the very young of *Cookeolus* appar-tly live in the upper layers of the water d are transported by ocean currents. Al-ough badly digested, a 37-mm specimen RHG) from the stomach of a specimen of *hunnus albacares* Bonnaterre clearly be-ngs to this species on the basis of the char-ters used in the introduction and in the y in this paper. The example is particu-rly noteworthy in that it establishes the esence of the long-rayed pelvic and soft rsal and anal fins on specimens down to is size, establishes a pelagic habitat for e very young, is the smallest individual corded from the western Atlantic, and is ly the seventh specimen recorded from the stern North Atlantic (in addition to those referred to in this paper, Schomburgk, 1848: 14, listed a specimen from Barbados and gave vertical fin-ray counts which confirm his identification).

Key to Western Atlantic Priacanthidae

A. Lateral-line scales 31 to 39; mid-lateral scale rows 35 to 43; dorsal soft-rays 10 to 12 (usually 11); anal soft-rays 9 to 11 (usually 10); first arch gillrakers 6 to 9 + 17 to 21, total 23 to 30 ..... *Pseudopriacanthus altus*

AA. Lateral-line scales 52 to 72; mid-lateral scale rows 58 to 85; dorsal soft-rays 12 to 15; anal soft-rays 12 to 16 ..*B.*

B. Mid-lateral scale rows 58 to 62; lateral-line scales 52 to 57; dorsal soft-rays 12 or 13; anal soft-rays 12 or 13; first arch gillrakers 6 or 7 + 17 to 19, total 23 to 25 ..... *Cookeolus boops*

BB. Mid-lateral scale rows 71 to 85; lateral-line scales 54 to 72; dorsal soft-rays 13 to 15; anal soft-rays 14 to 16 ..... (*Priacanthus*) ..... *C.*

C. First arch gillrakers 5 + 16 to 18, total 21 to 23; dorsal soft-rays 13; anal soft-rays 14; lateral-line scales 54 to 62; mid-lateral scale rows 72 to 82 ..... *Priacanthus cruentatus*

CC. First arch gillrakers 6 to 8 + 21 to 26, total 27 to 33; dorsal soft-rays 13 to 15 (usually 14); anal soft-rays 14 to 16 (usually 15); lateral-line scales 61 to 72; mid-lateral scale rows 71 to 85 ..... *Priacanthus arenatus*

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16

A PHOTOMICROGRAPHIC ADAPTER
OR STEREOMICROSCOPES USEFUL
N PHOTOGRAPHING FISH LARVAE.—
uring the course of a biological inventory
the waters off the southeastern United
ates, conducted by the U. S. Bureau of
ommercial Fisheries, it became necessary to
ake photographs of larval fishes collected
plankton tows. Numerous photographs
ere necessary for purposes of identification
d cataloging.

Most of the larvae were 15 mm or less in
ngth. Specimens of this size were generally
o large to photograph through a com-
ound microscope, and too small for effective
notographic results with cameras equipped
ith bellows and extension tubes. Because
the physical nature of a binocular system,
which an optically perfect single tube
nage cannot be produced with a stereomicro-
ope to satisfy their high manufacturer's
andards, the major optical companies could
ot supply an adapter for mounting a cam-
a on a single tube of a stereomicroscope
ith eyepiece in place. A single tube image
om such a system results in one side of a

flat field at the stage being *slightly* out of focus in relation to the other side (resolved when both tubes are used stereoptically). However, we found that the depth of field through the camera system was sufficient to overcome this to a point where satisfactory photographs of the relatively thin-bodied fish larvae could be achieved.

As the stereomicroscope was the most suitable instrument for studying larval fish, we modified a device suggested by Mr. Harvey R. Bullis, Jr., of the U. S. Bureau of Commercial Fisheries, which provides a simple adapter for mounting a single-lens reflex camera directly to one eyepiece barrel. Workers in many fields should find such a simple and inexpensive attachment useful in bridging the gap left by conventional photographic equipment.

While our device was designed for a specific camera and stereomicroscope combination, it would be adaptable for any combination of make of scope and single-lens reflex camera. The attachment consists of a brass tube designed to fit over the barrel of one of the eyepieces of the stereomicroscope. The eyepiece of the scope is left in place, contrary to the conventional photographic set-up for most microscopes, and the tube is designed to bring the lens of the camera almost into contact with that of the eyepiece of the microscope (as with the human eye in normal use of a scope). The brass tube is slit near one end and fitted with a thumbscrew to permit tightening when in place on the scope barrel. The

Fig. 1. Photomicrographic adapter (lower) with lens filter adapter (upper) for attachment of camera to eyepiece barrel of stereomicroscope. Drawn by Robert Wade.

opposite end of the brass tube is threaded to receive the female portion of a lens filter adapter of the series appropriate for the camera to be used, which in turn screws into the lens of the camera. No part of the camera lens is removed. Our 50-mm, 3.5 lens was used satisfactorily. The device is illustrated as Fig. 1.

We used no special lighting, but by trial and error found that with the lens open wide and a shutter speed of 1/25 of a second, the standard scope illuminators were sufficient for proper exposure with a panchromatic film having an ASA tungsten rating of 64 (daylight 80).

Focusing is done directly through the camera ground glass viewfinder, not through the eyepiece in the other barrel of the scope. Combinations of eyepieces and objectives can be varied for the desired magnification.

The stereomicroscopes at our disposal were very sturdy, but some of the newer models are of much lighter construction. The mounting of a heavy camera on the inclined ocular tube may thus pull the tube out of line, and in addition may make these lighter scopes rather unstable. Therefore, in mounting a camera, these factors should be considered, and where required, some extra outside support designed to remedy them.

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WATER CHEMISTRY AND POLLUTION

DISSOLVED OXYGEN IN LAKE ERIE, PAST AND PRESENT

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Abstract

Data presented on dissolved oxygen in Lake Erie in 1928-61 include a brief summary of records from each of the major limnological surveys made during the period and charts indicating areas where dissolved-oxygen deficiencies have been detected. Critically low concentrations of dissolved oxygen may have existed at the time of some of the earlier studies, but may not have been detected because of shortcomings in the sampling technique, the infrequency of sampling, and the lack of samples from some areas. Oxygen depletion in the central basin appears to have become gradually more extensive over the last three decades. At the present time, hundreds of square miles of the bottom waters have no detectable dissolved oxygen during part of the year. The vertical distribution of oxygen is affected sharply by the temperature gradient. In the absence of a metalimnion the percentage saturation of oxygen near the bottom is usually 60% or greater.

INTRODUCTION

Interest has increased the past few years in general environmental conditions in Lake Erie—particularly in dissolved oxygen (DO). This concern has been stimulated by two closely related recent occurrences: a near catastrophic change in bottom fauna, and the discovery that large areas of the bottom waters of the lake have no detectable dissolved oxygen during part of the year.

Interest was high in environmental conditions in Lake Erie also in the 20's, when two large-scale studies were made to determine whether pollution was the cause of a marked decline in the populations of some of the more desirable species of fish. Research by Wright (1955) in the western basin and Fish *et al.* (1960) in the central and eastern basins together comprise the most comprehensive limnological inventory of Lake Erie which has been made to date.

So few limnological investigations have been made in the open waters of Lake Erie that it is not possible to describe most of the progressive environmental changes in any detail. I will attempt, however, to show the general oxygen conditions at specific times, and their possible relation to present conditions, by briefly reviewing some of the studies in chronological order. Original data collected in 1961 are also included.

Lake Erie is divided morphometrically and limnologically into three distinct basins: a shallow western basin with several large and small islands, a large flat central basin of intermediate depth, and a deep eastern basin. An approximate boundary between the western and central basin is a line extending from Pelee Point to Pelee Island, to Kelleys Island, and to the eastern tip of the Marblehead Peninsula (Fig. 1). The boundary between the central and eastern basins extends from Long Point, Ontario, to Erie, Pennsylvania. Oxygen conditions are treated separately for each basin because of the marked limnological differences among the three regions of the lake.

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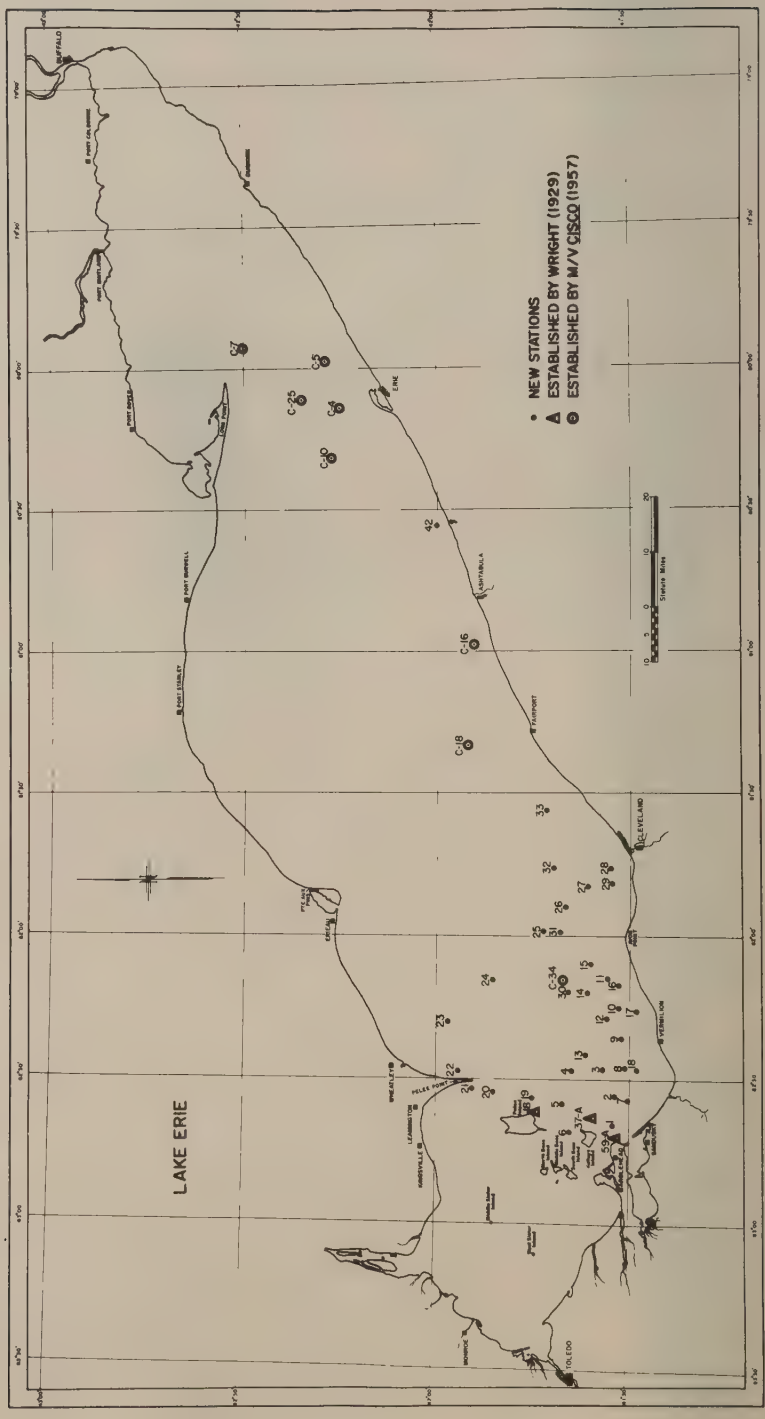

Fig. 1. 1961 Chemical Stations.

WESTERN BASIN

The western basin has been studied more intensively than the other two sins. A summary of four of the many investigations will serve, however, to scribe oxygen conditions in the approximately 30-year period during which the fferent studies were made.

Wright (1955) found no evidence of pollution in the open waters of the estern basin in 1928-30. Dissolved oxygen was not below 80% of saturation at e surface or below 70% in the bottom waters.

Studies by Chandler (1940, 1942, 1944) in the island section of the western sin in 1938-40 showed no significant change in DO from that reported by right. He stated (1944) that, "Oxygen in western Lake Erie is never at any ne seriously depleted and its vertical distribution is essentially uniform."

A significant change in DO was first detected in Lake Erie in September 53, when a period of little wind and high temperature led to thermal stratifi- tion over wide areas in the western basin. The stratification was accompa- ed by a serious reduction in DO in the hypolimnetic zone. Britt (1955a) re- rted that maximum DO during a three-day period was only 1.2 ppm at a ation near South Bass Island. The lowest DO which he recorded was 0.7 ppm ne lowest level reported by that date in any of the open waters of Lake Erie), a station 2 miles west of the island. After about five days, when water rculation had been restored in the area, the DO in the bottom water was ove 4 ppm. Britt found, however, that this short period of stratification and w DO had resulted in a drastic reduction of the mayfly *(Hexagenia)* popula- n. The entire population of mayfly nymphs was wiped out in some areas— en where more than 1,000 per square meter were found by Wood in 1952 ritt 1955a). In an area between the Canadian shore and Catawba Island the erage number of mayflies was reduced from more than 300 per square meter 44 (Britt 1955a). By 1954, however, the mayfly population had almost com- etely recovered (Britt 1955b).

No critically low DO conditions were found in 1957 and 1958, when the re- arch vessel *Cisco* carried on an investigation in the area in which Britt's udy was conducted. Beeton (1961) reported, however, that the density of may- nymphs was less than 40 per square meter. It appears, therefore, that oxy- n depletion to critical levels may have occurred again after the 1954 recovery. ygen demand in the waters and/or bottom muds of western Lake Erie ap- ars to be sufficiently great to reduce the DO rapidly in the bottom waters enever complete circulation is inhibited.

CENTRAL BASIN

Dissolved oxygen in the surface water in 1928-30 ranged from 7.6 to 12.6 m and the percentage saturation from 86 to 111 at three stations in the cen- al basin studied by Wright (1955); in the bottom waters the range was 0.8 to .5 ppm and 9-105% saturation. The 0.8 ppm value was at station 59-A ig. 1) in August 1930 after a period of thermal stratification. At station -A, east of Kelleys Island, on the same date the water was thermally strati- d and DO was below 5 ppm. Two other low readings were recorded by right in 1928—62% of saturation at station 59-A and 65% at station 18. The ter was thermally stratified at each station.

The 1929 survey of the central basin by Fish *et al.* (1960) included month- cruises in June-September; water samples were collected at about 25 stations ring each cruise. For the present discussion of this survey, an arbitrary

value of 65% of saturation or less is used to identify areas of low DO. No oxygen levels below 65% were found during June or September, but oxygen d ficiencies were observed during July and August. In July, bottom water con taining 65% or less DO was found at seven stations (six in the north-central section of the central basin and one about 12 miles northwest of Fairport, O The lowest DO (50% of saturation) was at a station 3 miles off Port Burwell Ontario. In August, the bottom waters at six stations (four of which had an oxygen deficiency in July) had less than 65% DO saturation; the two lowest p centages were 44 and 42. Seven of the nine different stations with oxygen d ficiencies during July and/or August were within a triangular area bounded b Rondeau on the north shore and Cleveland and Fairport on the south. The wa was over 60 ft deep at all nine stations and was thermally stratified. The 1 survey demonstrated for the first time the occurrence of thermal stratificati which may last for several weeks, over a large portion of the central basin.

It is possible that the concentration of DO was lower in 1929 than the records indicated, for the following reasons: water samples were collected 1 meter or more off the bottom and thus were not always taken below the metalimnion; samples were collected only once a month; and no water sampl were taken from the southwestern corner of the central basin, where the low levels of dissolved oxygen were found in later years. Although Fish *et al.* (1960) concluded that pollution was extremely light or nonexistent, these poss ble deficiencies in technique and coverage, together with the observations in later years, suggest that Lake Erie was beginning to show signs of eutrophic tion as early as 1929.

Investigations in 1947-53 by the University of Western Ontario, in the same general area in which oxygen deficiencies were found in 1929, showed l values consistently lower than those reported by Fish *et al.* (1960). The mo intensive sampling during these years revealed that the dissolved-oxygen con centration in bottom waters in midsummer was often less than 40% of satura tion and even as low as 20% (Powers *et al.* 1960) in the thermally stratified north-central portion of the central basin.

An extensive zone of low oxygen was first found in the southwestern po tion of the central basin in 1958 by the *Cisco,* during a period of apparently normal meteorological conditions. The DO in the bottom waters was below 3 ppm for more than 3 weeks at a station 7 miles north of Huron, Ohio (C- Fig. 1). At another station 15 miles north of Lorain, Ohio (C-34), the DO w below 3 ppm over 4 weeks. The lowest reading recorded at the latter statio was 1 ppm, in late August. The oxygen level was probably even lower at th bottom, however, because the metalimnion and hypolimnion were so narrow t it was not possible to sample the desired level with conventional water sam- plers. A temperature of 17.7°C was registered on the reversing thermomete attached to the Nansen bottle with which the late-August sample was taken. T bathythermograph tracing made at the time of sampling showed that this tem perature was in the metalimnion, at a depth of 54 ft (Fig. 2). Since the Nan bottle is 24 inches long and the metalimnion was only 36 inches thick, the wa sample represented a vertical sample which included two-thirds of the entire metalimnetic layer. The sample was therefore a composite of the water in that zone rather than from a single narrow stratum. This type of extreme t perature gradient was typical in the central basin in 1958 (and also during Ju and August 1961).

A synoptic survey of the central basin in early September 1959 and a la wide survey in late August 1960, made by biologists aboard vessels from sev eral agencies, yielded further information on the geographical extent of oxyge deficient waters in the central basin. In 1959, less than 1.0 ppm DO was fou

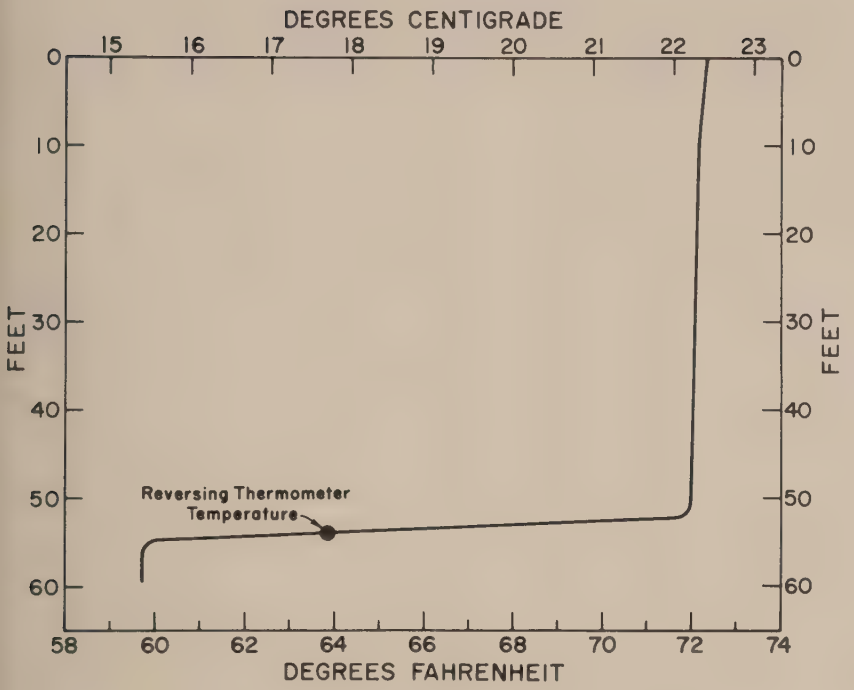

Fig. 2. Thermal profile station C-34, 27 August 1958.

approximately 1,390 square miles of Lake Erie, or slightly over 14% of the tal area (Fig. 3).[1] In 1960, the area with less than 1 ppm DO was about 1 square miles—slightly less than half the area in 1959—but the oxygen-ficient region extended somewhat farther east than in 1959 (Fig. 3). The obable reason for the greater oxygen deficiency in 1959 was the longer peri- of thermal stratification over a much wider area.

The synoptic surveys of 1959 and 1960 revealed the severe oxygen deple-on that had developed in the central basin of Lake Erie, and indicated the verity and geographical extent of this condition. These and earlier observa-ons showed also that appreciable reduction of DO apparently does not occur Lake Erie unless the water is stratified. Almost invariably the severe oxy-en depletion in the hypolimnion was below a thin metalimnion with a sharp mperature gradient. Under normal weather conditions, oxygen deficiencies ould not be expected in shoal areas, or in the deeper waters of the central sin in the early summer. Britt (1955a) showed what can happen in the west-rn basin when weather conditions are unusual.

A series of detailed observations on concentration of DO in central Lake rie were made in April-September 1961. Thermal stratification and low oxy-en were first detected during the week of 11-14 July, in the southwestern rner of the central basin, at stations with water depths greater than 25 and ss than 50 ft. The lowest DO recorded was 1.7 ppm (Table 1) in a sample

[1] Based on tabulation by Mr. Nelson Thomas of the Ohio Division of Wildlife of material forwarded to him by the cooperating agencies. These same records were used to construct Figure 3.

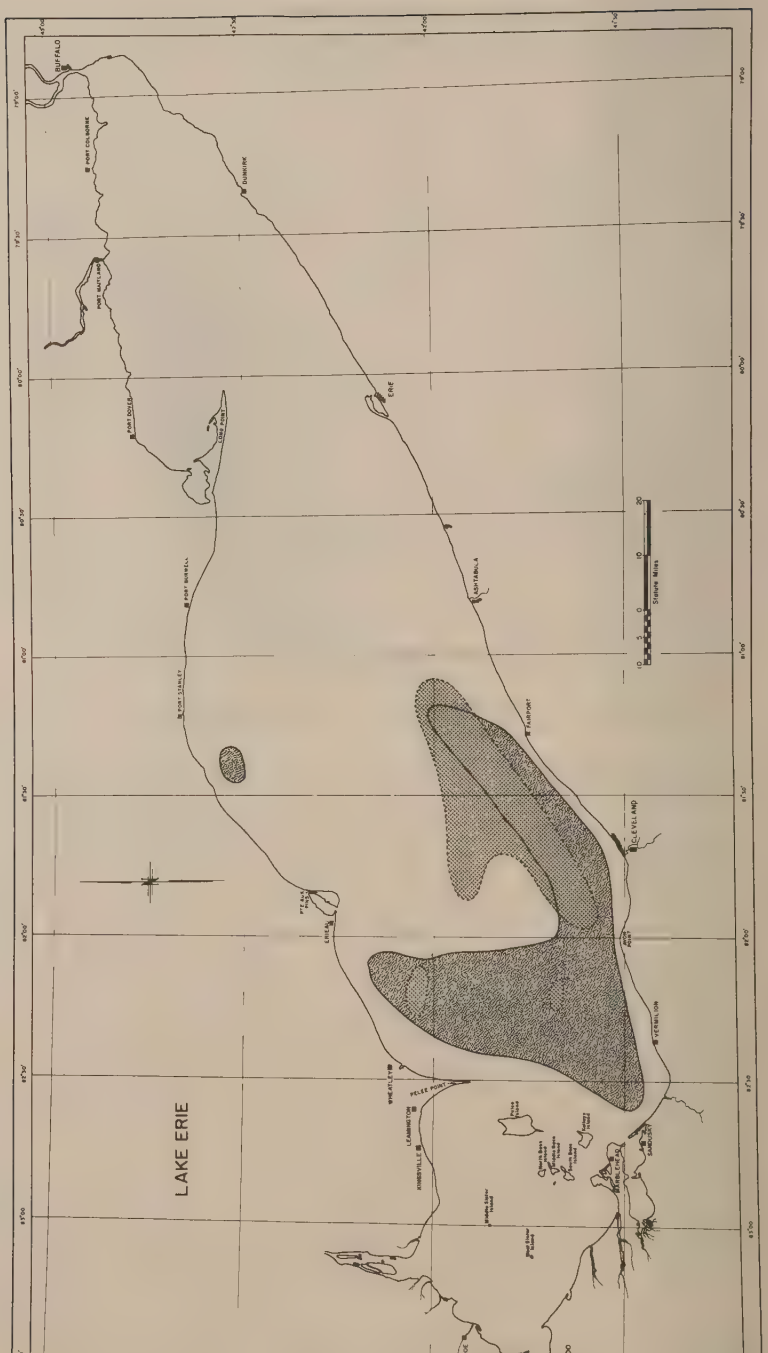

Fig. 3. Areas with less than 1 ppm DO during synoptic surveys of 1959 and 1960. (Solid isopleth, September 4-5, 1959; dotted isopleth, August 30-31, 1960.)

Table 1. Summary of Chemical and Temperature Data Collected in Lake Erie, 1961

ation mber	Date	Time (EST)	Depth (feet)		Water temperature (°C)	Dissolved oxygen		Alkalinity (ppm)	
			Total	Sample		ppm	Percentage saturation	Phenol-phthalein	Methyl orange
1	Apr. 13	1420	35	0	3.8	12.2	98	0	82
				33	3.8	12.0	96	0	98
9-A	Apr. 13	1500	30	0	3.6	12.0	96	0	90
				28	3.8	11.8	95	0	91
2	Apr. 14	0945	46	0	3.8	12.3	99	0	88
				42	3.5	12.3	99	0	87
3	Apr. 14	1030	46	0	3.3	12.4	99	0	103
				42	2.9	12.4	97	0	103
4	Apr. 14	1110	48	0	2.4	12.6	98	0	102
				44	2.3	12.6	98	0	101
5	Apr. 14	1215	41	0	2.5	12.6	98	0	101
				37	2.4	12.6	98	0	99
6	Apr. 14	1255	40	0	3.6	13.0	103	0	87
				36	2.7	12.4	96	0	100
7-A	Apr. 14	1330	42	0	3.8	12.6	99	0	92
				38	2.5	12.6	95	0	100
9-A	Apr. 26	1330	30	0	8.2	11.7	102	0	88
				20	8.0	11.7	102	0	86
7	Apr. 27	1000	41	0	6.9	12.5	105	0	84
				36	6.8	12.1	102	0	84
8	Apr. 27	1055	41	0	6.9	12.7	107	0	86
				36	6.5	11.8	99	0	84
9	Apr. 27	1125	43	0	7.9	12.1	107	0	87
				37	7.2	11.8	100	0	86
10	Apr. 27	1230	40	0	8.0	12.6	109	0	87
				34	6.6	12.4	104	0	87
11	Apr. 27	1305	55	0	6.6	11.8	99	0	95
				48	5.4	11.6	95	0	94
12	Apr. 27	1415	45	0	6.2	11.9	99	0	94
				37	5.3	11.8	97	0	93
7-A	Apr. 28	1010	42	0	7.0	12.3	104	0	85
				38	5.8	11.7	96	0	91
5	Apr. 28	1050	42	0	6.8	12.3	103	0	85
				36	5.9	12.1	102	0	91
(1930 ation)	Apr. 28	1130	24	10	7.1	12.7	107	0	83
7-A	May 8	1435	42	0	10.3	12.5	115	0	84
				39	8.6	11.2	99	0	85
9-A	May 8	1530	33	0	11.2	10.7	101	0	92
				29	9.7	10.1	92	0	...
7-A	June 16	1435	43	0	20.0	8.3	95	0	87
				33	17.2	8.0	87	0	90
9-A	June 16	1525	32	0	20.8	7.7	89	0	93
				28	18.4	7.6	83	0	...
1	July 10	1415	36	0	23.4	8.5	102	2	93
				30	20.0	5.5	62	0	97
7-A	July 10	1510	42	0	23.1	8.2	98	3	95
				35	20.4	8.0	91	2	95
1	July 11	0930	38	0	21.1	8.2	95	3	98
				31	20.7	7.4	87	0	106
2	July 11	1115	42	0	22.2	8.1	94	3	94
				37	20.6	7.9	91	1	94
8	July 11	1200	45	5	20.8	8.6	99	5	95
				35	20.4	8.1	93	3	95
10	July 11	1400	50	0	22.4	8.5	100	2	96
				44	19.3	7.1	80	0	100
1	July 12	1225	32	0	22.8	7.7	91	2	99
				29	21.3	7.4	86	3	97
1	July 14	0930	36	0	21.4	7.8	91	2	98
				29	18.5	2.9	32	0	99
4 mi. N of 1	July 14	1015	33	32	18.5	1.7	18	...	...
4 mi. E of 1	July 14	1030	39	33	18.4	2.8	30	...	...

Table 1. Continued

Station number	Date	Time (EST)	Depth (feet)		Water temperature (°C)	Dissolved oxygen		Alkalinity (ppm	
			Total	Sample		ppm	Percentage saturation	Phenol-phthalein	Me ora
37-A	July 14	1145	42	28	21.2	8.1	94	...	..
				33	21.2	8.0	93	...	..
				38	20.6	6.5	74	...	..
				41	19.0	4.5	50	...	..
1/2 mi. S of 1	July 14	1240	32	31	19.0	4.2	46	...	..
1	July 24	1400	36	0	23.5	8.2	99	...	..
				25	23.1	8.2	98	...	..
				28	21.5	8.0	93	...	..
				30	17.8	0.8	8	...	..
				32	17.7	0.6	7	...	..
1 mi. S of 1	July 24	1530	32	29	17.7	0.8	8	...	..
2 mi. S of 1	July 24	1540	28	27	18.5	2.1	23	...	..
3 mi. S of 1	July 24	1555	28	19	20.7	3.6	42	...	..
1	July 25	0940	34	16	22.9	7.6	91	...	..
				21	22.8	7.4	88	...	..
				26	18.2	1.8	19	...	..
				32	18.2	1.8	19	...	..
37-A	July 25	1020	42	30	23.1	7.5	90	...	..
				35	18.4	1.8	19	...	..
				41	18.4	1.8	19	...	..
13	July 25	1138	47	38	19.2	4.2	47	0	
				42	18.3	2.8	30	0	
14	July 25	1303	51	25	22.8	8.2	98	...	..
				40	17.6	2.2	23	...	..
				45	16.3	2.0	21	...	..
15	July 25	1350	53	39	20.8	8.0	92	...	..
				44	15.1	1.1	10	...	..
				49	15.0	1.0	9	...	..
16	July 26	0940	48	30	23.3	8.1	98	...	..
				33	23.1	8.1	97	...	..
				38	18.4	1.4	14	...	..
				43	17.4	0.8	8	...	..
17	July 26	1145	45	36	21.4	2.9	34	...	..
				41	16.0	0.2	2	...	..
18	July 26	1301	43	30	22.6	7.3	87	...	..
				34	17.6	0.6	5	...	..
				39	17.4	0.6	5	...	..
7	July 26	1348	36	23	23.2	7.9	95	...	..
				27	22.3	5.4	63	...	..
				31	18.3	0.2	2	...	..
37-A	July 26	2100	42	1	24.3	8.5	104	...	..
				30	22.7	4.8	57	...	..
				35	18.4	1.6	17	...	..
				39	18.2	1.0	10	...	..
37-A	July 26	2300	42	1	24.2	8.5	104	...	..
				30	23.2	7.9	95	...	..
				35	20.1	2.4	27	...	..
				39	18.2	0.9	9	...	..
37-A	July 27	0000	42	1	24.1	8.5	103	...	..
				30	23.2	7.9	95	...	..
				35	19.7	2.7	30	...	..
				39	18.2	1.2	13	...	..
37-A	July 27	0100	42	1	24.0	8.5	103	...	.
				30	23.2	8.0	96	...	.
				35	19.8	2.8	31	...	.
				39	18.2	1.2	13	...	.
37-A	July 27	0200	42	1	24.0	8.6	105	...	.
				30	23.2	8.0	96	...	.
				35	20.0	5.0	56	...	.
				39	18.2	1.5	16	...	.
37-A	July 27	0300	42	1	23.9	8.5	105	...	.
				30	23.2	8.1	96	...	.
				35	21.3	5.1	59	...	.
				39	18.2	1.0	10	...	.

Table 1. Continued

tion nber	Date	Time (EST)	Depth (feet)		Water temperature (°C)	Dissolved oxygen		Alkalinity (ppm)	
			Total	Sample		ppm	Percentage saturation	Phenol-phthalein	Methyl orange
-A	July 27	0400	42	1	23.9	8.6	105	...	...
				30	23.2	8.0	96	...	...
				35	19.3	1.1	12	...	...
				39	18.2	0.9	9	...	...
-A	July 27	0500	42	1	23.9	8.5	105	...	...
				30	23.0	7.8	93	...	...
				35	18.4	1.2	13	...	...
				39	18.2	1.0	10	...	...
-A	July 27	0600	42	30	23.1	7.8	94	...	...
				35	18.6	1.3	14	...	...
				39	18.3	1.2	13	...	...
5	July 27	0745	40	29	23.2	7.8	94	...	...
				33	22.8	6.8	81	...	...
				37	18.3	1.9	20	...	...
9	July 27	0825	34	26	23.0	6.7	80	...	...
				30	20.1	1.4	15	...	...
0	July 27	0910	26	0	24.8	5.7	70	...	...
				19	23.9	5.9	71	...	...
				23	23.5	5.2	62	...	...
1	July 27	1015	36	13	24.0	7.4	90	...	...
				20	18.6	6.2	68	...	...
				34	17.6	5.9	64	...	...
1	July 27	1350	32	15	22.9	8.7	104	...	...
				20	22.4	7.4	87	...	...
				28	21.0	4.8	55	...	...
-A	Aug. 15	1515	42	1	23.9	8.2	100	3	102
				38	22.3	4.8	56	0	102
				41	18.9	1.2	13	...	...
1	Aug. 22	0935	33	28	22.6	7.3	85	3	94
				32	22.0	7.0	82	...	...
-A	Aug. 22	1010	42	38	22.6	7.2	85	2	96
5	Aug. 22	1052	41	37	21.6	7.4	86	2	97
1	Aug. 22	1325	33	24	21.4	5.6	65	0	101
				29	21.2	5.0	58	0	98
2	Aug. 22	1513	41	32	20.0	8.2	93	0	103
				37	20.1	8.2	93	0	93
4	Aug. 24	0945	61	44	18.3	5.7	62	...	...
				49	14.7	2.0	20	...	...
				54	14.2	0.9	9	...	...
4	Aug. 24	1110	68	54	14.1	1.6	15	...	...
				59	14.2	1.6	15	...	...
				64	14.0	1.4	14	...	...
5	Aug. 24	1235	70	54	16.2	2.7	28	...	...
				61	14.4	0.1	1	...	...
				66	14.3	0.0	0	...	...
5	Aug. 24	1325	68	44	22.3	8.0	95	...	...
				54	16.0	1.5	15	...	...
				64	14.5	0.0	0	...	...
7	Aug. 24	1420	62	42	22.0	7.8	91	...	...
				47	16.0	0.8	8	...	...
				57	15.3	0.0	0	...	...
8	Aug. 24	1515	52	43	22.4	6.9	81	...	...
				48	22.2	6.3	76	...	...
9	Aug. 25	0910	50	41	22.3	5.7	66	...	...
				46	21.4	5.1	60	...	...
4	Aug. 25	1140	60	47	21.2	3.3	38	...	...
				52	15.9	0.0	0	...	...
				56	15.4	0.0	0	...	...
A	Sept. 19	0945	45	38	21.8	7.0	81	0	99
0	Sept. 19	1215	64	50	21.3	7.3	85	3	96
				55	17.0	0.5	4	0	98
				60	13.8	0.0	0	0	100
1	Sept. 19	1340	72	55	21.2	7.2	83	...	...
				58	14.9	0.2	3	0	98
				63	14.0	0.1	1	...	...
				68	14.0	0.1	1	0	99

Table 1. Continued

Station number	Date	Time (EST)	Depth (feet)		Water temperature (°C)	Dissolved oxygen		Alkalinity (ppm)	
			Total	Sample		ppm	Percentage saturation	Phenol-phthalein	Meth oran
32	Sept. 19	1450	74	57	21.6	7.1	83	...	...
				64	19.8	3.1	35	...	...
				69	14.5	0.2	2	...	...
33	Sept. 19	1620	66	52	21.6	7.2	84	...	...
				62	16.0	0.2	2	...	...
C-18	Sept. 20	0915	75	62	21.8	7.2	85	0	99
				67	21.9	...	...	...	...
				71	21.7	7.0	82	0	97
				74	16.1	1.6	16	...	...
C-16	Sept. 20	1145	59	53	21.6	7.3	85	...	...
				55	19.1	3.7	41	...	...
				58	16.4	0.6	6	...	...
34	Sept. 20	1430	45	42	20.9	7.6	88	...	...
				44	20.9	6.8	79	...	...
C-5	Sept. 21	0845	59	49	21.3	7.8	90	...	...
				55	21.1	7.2	83	...	...
C-25	Sept. 21	1040	100	80	15.6	6.5	67	...	...
				90	14.5	6.3	63	...	...
				96	12.3	5.5	53	...	...
C-10	Sept. 21	1228	53	49	21.2	7.3	85	...	...
C-4	Sept. 21	1345	67	53	21.5	7.3	85	...	...
				58	21.4	7.2	84	...	...
				63	13.8	3.7	37	...	...
				65	12.8	...	...	...	...
C-7	Sept. 22	1320	210	0	22.0	7.5	88	...	...
				97	11.7	6.4	61	...	...
				204	6.8	5.5	47	...	...

taken 1 ft off the bottom at station 1 (Fig. 1), 3 miles north of Sandusky ligh The metalimnion at this station extended to the bottom. Had the water been deep enough for a hypolimnion to be present, the DO just above the bottom a most surely would have been lower.

Low oxygen concentrations in the bottom waters extended over a wide a during the week of 24-28 July. Thermal stratification was well developed at stations where water depth exceeded 30 ft. Oxygen in the hypolimnion was below 25% of saturation at all stations except in the Pelee Point area (statio 20 and 21, Table 1). Two samples from station 1 (Fig. 1) illustrate the mag nitude of differences possible between two closely adjacent levels: a sample from the top of the metalimnion contained 8.0 ppm DO, whereas a sample tak 2 ft below the first sample, in the hypolimnion, contained only 0.8 ppm.

By 22 August 1961 oxygen and thermal conditions were considerably changed from the mid-July period. Dissolved oxygen was high and the water was homothermous at all stations with water depths less than 50 ft. The du tion of stratification (Fig. 4) and low oxygen at these shallower stations had been 15 to 35 days. Samples at six stations (23-28, Table 1) on a transect b tween Wheatley, Ontario, and Cleveland, Ohio, revealed, however, that the DO the hypolimnion (in water more than 50 ft deep) was less than 1 ppm for a linear distance of at least 35 miles, and not detectable over a distance of at least 15 miles (Table 1). This area without detectable oxygen was several miles north of any oxygenless area found during the synoptic surveys of 1959 and 1960.

Samples were collected 19-22 September 1961 at a series of stations in the southern half of the central basin, between Kelleys Island and Erie, Pa.

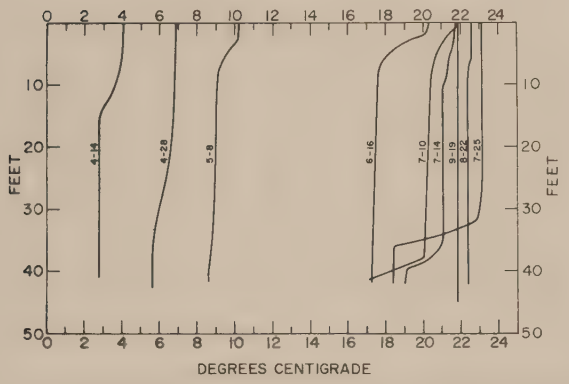

Fig. 4. Thermal development—station 37-A, 1961.

hermal conditions were similar to those in late August, in that stratification as limited to areas deeper than 50 ft. The temperature gradient of the etalimnion in the deeper areas was the sharpest encountered during the year; mperature changes greater than 5°C per foot were observed at several locaons (Table 2). Dissolved oxygen was below 1 ppm between an area north of orain to Ashtabula, Ohio, a distance of about 70 miles.

Table 2. Depth, Temperature, and Thermal Gradient of the Metalimnion, Lake Erie, September 19-22, 1961

ation mber*	Depth (feet)			Temperature (°C)			Rate of temperature change (°C per foot)	Total depth at station (feet)
	Top	Bottom	Thickness	Top	Bottom	Difference		
30	53	57	4	21.8	14.1	7.7	1.9	64
31	55	56	1**	21.2	13.9	7.3	7.3	72
32	61	62	1**	21.6	14.5	7.1	7.1	74
33	58	59	1**	21.6	16.1	5.5	5.5	66
C-18	70	72	2	21.7	16.1	5.6	2.8	75
C-16	54	55	1**	21.6	16.6	5.0	5.0	59
C-25	68	90	22	21.5	12.3	9.2	0.4	100
C-4	57	60	3	21.3	12.8	8.5	2.8	67
C-7	80	130	50	21.6	6.8	14.8	0.3	210

Station number and (in parentheses) total depths of water for stations at which a metalimnion was not present are as follows: 37-A (45); 34 (45); C-5 (59); C-10 (53); and C-9 (50).

No detectable depth change on bathythermograph tracing in metalimnion.

The 1961 investigation in the central basin can be summarized as follows. ratification and low DO first occurred in early July and were still present e last week in September. The DO was substantially reduced at every staon which showed a sharp temperature gradient; temperature changes of sevral degrees per foot were common in the deeper areas. Bottom waters in ertain areas were without detectable DO for periods of several weeks. Areas ith less than 1 ppm DO in the bottom water probably included more than 75% the central basin. Oxygen depletion did not appear to be gradual; instead, e DO seemed to be consumed almost immediately after stratification. The xygen-reducing substances are in the bottom muds and not suspended in the ater. Specialized equipment is needed to collect satisfactory water samples the hypolimnion is thin.

Table 3. Summary of Chemical and Temperature Data Collected in Deep Hole of the Eastern Basin of Lake Erie

Date	Depth (feet)		Water temperature (°C)	Dissolved oxygen		Alkalinity (ppm)		pH	Source of data
	Total	Sample		ppm	Percentage saturation	Phenol-phthalein	Methyl orange		
Sept. 6, 1928	195	0	19.2	8.7	96	1.5	98	8.2	Wagner 1929
		185	9.0	10.0	88	0.0	100	7.8	
June 12, 1929	200	2	10.5	10.8	100*	1.5	97	8.1	Fish *et al.* 1960
		180	5.0	10.0	81*	0.0	101	8.1	
July 28, 1929	200	2	15.9	8.7	92*	2.3	100	8.2	" " "
		197	4.9	10.4	84*	0.0	99	7.8	
Aug. 9, 1929	202	2	21.0	8.7	100*	2.0	97	8.2	" " "
		194	5.2	10.4	84*	0.0	97	7.7	
Sept. 7, 1929	197	2	20.8	8.9	103*	3.0	95	8.3	" " "
		190	5.5	10.0	82*	0.0	94	7.6	
July 6, 1950	197	0	17.9	...	...	2.0	110	8.2	Powers *et al.* 1960
		190	3.9	8.2	64	0.0	106	7.6	
Aug. 10, 1950	180	0	20.1	8.8	100	1.5	104	8.2	" " "
		150	4.0	8.2	64	0.0	105	7.5	
July 3, 1951	197	0	20.2	9.2	105	0.0	104	8.0	" " "
		190	4.0	11.2	88	0.0	109	7.5	
Aug. 9, 1951	190	0	21.1	8.9	103	4.0	106	8.2	" " "
		185	4.4	10.0	79	0.0	106	7.9	
July 9, 1957	200	190	5.5	10.4	85	...	...	...	Present study
Aug. 19, 1957	200	0	22.5	8.4	100	...	...	...	" "
		180	5.8	7.6	62	...	...	...	
Sept. 28, 1957	200	0	17.5	9.5	103	...	...	...	" "
		180	6.4	6.8	57	...	...	...	
Oct. 25, 1960	200	5	14.5	11.1	113	...	...	8.1	Kramer 1961
		195	8.8	9.1	81	...	...	7.2	
Sept. 22, 1961	210	0	22.0	7.5	88	...	...	...	Present study
		204	6.8	5.5	47	...	...	...	

EASTERN BASIN

Critically low DO has not been reported to date in the open waters of the stern basin. Data collected in the "deep hole" area appear to indicate, however, that the oxygen demand in bottom waters has increased during the past years. In four samples collected in 1928 and 1929, the DO in bottom aters ranged only from 10.0 to 10.4 ppm or 81 to 88% saturation (Table 3). ata for subsequent years do not show progressively lower DO, but definite anges are indicated. These changes are apparent even though the wide difrence in DO on approximately the same dates in 1950 and 1951 (Powers *et al.* 60) indicated considerable annual variation in oxygen depletion. On 22 Septmber 1961 the DO in the hypolimnion at station C-7 was only 5.5 ppm (47% saturation).

As late as October 1960, the bottom temperature in the deep hole was low 9°C (Kramer 1961) and bottom temperatures in September of 1929, 1957, d 1961 were below 7°C. (In view of all of the post-1929 data it is difficult explain the high bottom temperature found in 1928 unless unusually strong nds had partially restored circulation.)

The 1961 data indicated not only increased oxygen consumption but also increase of roughly 1.5°C in bottom temperature. This change is in generagreement with Beeton's (1961) statement that the temperature in the entire ke has increased by about 2°C since 1918-27. Thus the lower oxygen conntration in 1961 may be partly a result of the lower solubility at the higher 61 temperature.

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MORPHOLOGIE UND FUNKTION
ES KIEFER–UND KIEMENAPPARATES
ON TIEFSEEFISCHEN DER GATTUN-
EN MALACOSTEUS UND PHOTOSTO-
IAS (TELEOSTEI, ISOSPONDYLI, STO-
IATOIDEA, MALACOSTEIDAE). By
laus Günther and Kurt Deckert. 'Dana'
eport 49, published by the Carlsberg
oundation, Copenhagen, 1959; 54 pp., 33
xt figs.—We are once again indebted to
rofessor Günther and Dr. Deckert for an-
her of their scholarly and provoking
udies on the functional morphology of
eding and respiration in predaceous deep-
a fishes. This paper is one of the most
cent in their series of contributions, pre-
ous numbers of which have contained dis-
ssions of this topic in *Gonostoma, Cyclo-
one, Chauliodus, Photostomias* and others.
the present paper the authors consider
o species of the stomiatoid family Mala-
steidae, which contains what are perhaps
e most highly specialized of all bathy-
elagic fishes (excepting the Lyomeri, which
e malacosteids curiously parallel in many
spects).

The mouth of malacosteids is essentially
floating spring trap. In setting the trap,
e cranium is pulled up and back. This
possible because the anterior vertebrae
e absent, and the skull is supported by
ly the elastic notochord, a condition which
also present, in varying degrees, in *Chauli-
lus, Idiacanthus,* and a number of melanos-
miatids. The very elongate, posteriorly
rected suspensorium is thus caused to
ing down and forward and the dentary is
ojected below and far in advance of the
anium. A strong muscular cord which
ns from the symphysis of the mandibles
the basihyal serves to snap shut the jaw
d trap the prey. Malacosteids are probably
nited to feeding on large prey (and this
borne out by examination of stomach con-
nts) because of one of the most striking
culiarities of this family, namely, the ab-
nce of a floor in the mouth. Food must
large enough to be snapped up in the
ap and large enough so that it will not
cape through the bottom of the floorless
outh. (The nature of the floorless mouth
an interesting side issue. Tchernavin, 1946, *Nature* 157:303, interprets part of the empty space in the floor of the mouth as a hyoid gill slit, and although he admits the structure is probably secondarily acquired he criticizes several authors for what he implies to be their naïve interpretation of this structure. Although it might be called a hyoid cleft on topographical grounds, it seems extremely improbable that it is homologous with the hyoid gill slit in Placoderms or in the Lyomeri, and it is interesting that Dr. Günther and Dr. Deckert refer to "der Verlust des Mundbodens.")

A section of the paper is devoted to problems of respiration. The opercular bones are absent or so greatly reduced that a functional opercle is absent. Branchiostegal membranes are also greatly reduced. These reductions, in addition to the lack of a floor in the mouth, tend to preclude the maintenance of a respiratory current over the gills. The authors discuss the possible importance as respiratory valves, of folds of membrane on parts of the hyoid arch (Tchernavin, *op. cit.,* has also suggested the importance of the "mandibular operculum" in the respiration of *Photostomias*). In view of the reduced gill filaments and the soft, naked skin in malacosteids it seems probable to the reviewer that respiration through the integument must play an important role in maintaining these fishes.

In presenting evidence for their ideas on the physiological aspects of feeding discussed in this paper, the authors have also given us a detailed picture of the cranial osteology and the anterior myology in *Malacosteus* and to a lesser extent in *Photostomias.* We must therefore also thank them for valuable descriptive and comparative morphology (with regrets that *Aristostomias,* the other genus in this family was not available for their studies).

In summary, comparative and descriptive morphologists, systematists, ecologists and physiologists should all find much of interest in this paper and also in the entire series of which it is a part. We wish the authors continuing success in their researches.—DANIEL M. COHEN, *Ichthyological Laboratory, Bureau of Commercial Fisheries, Washington, D. C.*

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PROCEEDINGS
OF THE
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ASTROBLEPUS PHOLETER, A NEW SPECIES OF CAVE-DWELLING CATFISH FROM EASTERN ECUADOR

By Bruce B. Collette
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The discovery of an essentially unpigmented, minute-eyed species of *Astroblepus* Humboldt in a cave in eastern Ecuador is of great interest because no cavernicolous species of Astroblepidae has previously been reported. Padre Pedro I. Porras G. of Mision Josefina, Tena, Ecuador collected the first known specimen and sent it to the U.S. National Museum where I have been permitted to study it. Upon learning that it was a new species, Padre Porras kindly wrote to me concerning the exact locality, life colors, and habitat of this heretofore unknown catfish and returned to the cave to collect three additional specimens which he graciously forwarded to me. The figures were drawn by Mildred H. Carrington of this Laboratory. Drs. Daniel M. Cohen, J. A. F. Garrick, and W. Ralph Taylor have read the manuscript and made valuable comments.

Astroblepus pholeter, new species
(Figs. 1–2)

Diagnosis: A species of *Astroblepus* (see Gosline, 1947: 92–93) which is pinkish-white in life; lacks bands, spots, or other pigmentation; has minute eyes (5.0–6.3 times in the interorbital distance); long filaments on the tips of the leading elements of the pectoral, dorsal, and caudal fins; a long maxillary barbel which reaches to the base of the pectoral fin; an elongated barbel on the nasal flap; and a well-developed spine in the adipose fin.

Description: Interobital distance slightly less than distance from eye to rear margin of posterior nostril; tip of adpressed pelvic fin reaching to anus or slightly beyond; prominent spine in adipose fin projecting beyond thin membrane connecting adipose to caudal peduncle; origin

FIG. 1. Lateral view of holotype of *Astroblepus pholeter*, new species.

of pelvic fins slightly posterior to origin of dorsal fin; teeth in outer row of upper jaw unicuspid except for 2–4 on each side of midline which are deeply bicuspid; teeth in posterior rows of upper jaw bicuspid; teeth in outer row of lower jaw mostly Y-shaped bicuspids; upper surface of head and body in front of origin of dorsal fin sparsely covered with small prickles; anus located two-thirds of distance posteriorly from pelvic origin to anal origin; pectoral filament reaching to anus; dorsal rays i,6; anal i,5 or 6; pectoral i,9 (i,10 on the right side of one specimen); pelvic i,4; and caudal 5+6 branched rays plus an upper and lower elongated and unbranched ray; vertebrae 26–27 (exclusive of anterior fused vertebrae).

As is the case in adult males of all species of *Astroblepus* examined, the single known male of *A. pholeter* has an elongate urogenital papilla which probably functions as an intromittent organ. However, the urogenital papilla of this male differs in being forked for the last 3.0 mm of its 8.1-mm length. Although it appears normal in other respects, additional males will have to be examined to see if a forked urogenital papilla is a distinguishing characteristic of *A. pholeter*.

In his definition of the Astroblepinae, Gosline (1947: 92–93) wrote "gill-rakers absent or rudimentary." I find that *A. pholeter*, like 16 other species of *Astroblepus* examined, have fairly well-developed gill-rakers. Gill-rakers are absent or rudimentary on the first arch, but well-developed ones are present on the more posterior arches. *A. pholeter* lacks gill-rakers on the first arch, has two or three poorly developed rakers on the second arch, and five to seven well-developed rakers on the last three arches.

Types: The holotype is USNM 196623, a female 62 mm in standard length (Figs. 1–2) collected in a large cave in Latas, 4 km north of Archidona, Napo Province, eastern Ecuador, by Padre Pedro Porras G. in 1961. The stream issuing from this cave empties into the Misagualli

FIG. 2. Dorsal view of head of holotype of *Astroblepus pholeter*, new species.

River which drains into the Napo River, a tributary of the Amazon. Paratypes from the same locality are USNM 196671, a male 64 mm SL and a female 66 mm SL, and Chicago Natural History Museum 63855, a female 57 mm SL, all taken on 28 January 1962 by Padre Porras.

Etymology: The Greek name *pholeter* means "one who lurks in holes," in reference to the cavernicolous habits of this species.

Comparisons: Astroblepus pholeter is very different from all other known species of *Astroblepus*. It appears to be the least pigmented species in the genus. Its eyes are much smaller than in most of the other species. Its pectoral filament, nasal barbel, and maxillary barbel are all more elongate than those in any of the other 31 forms in the key to the *Astroblepus* of northern South America presented by Schultz (1944: 278–282). The adipose spine is larger than in any of the species (at least 16) represented in the National Museum collection. *A. pholeter* differs strongly from the types of 13 species of *Astroblepus* in the collections of the U.S. National Museum and the Chicago Natural History Museum. It superficially resembles *A. longifilis* (Steindachner) in having long filaments on the dorsal and anal fins, long pelvic fins, and a barbel on the nasal flap. However, it differs markedly in its smaller eyes, lack of pigment, longer nasal barbel, longer pectoral filament, well-developed adipose spine, and lack of an adipose ridge extending from the posterior end of the dorsal to the base of the caudal fin.

Habitat and habits: Padre Porras has informed me that he has col-

lected *A. pholeter* only in the region of perpetual darkness in the cave, 300 m to 2 km from its mouth. He characterizes the waters of the stream as notably calcareous. The temperature was 15°C. These catfish hide in holes in rocks and are very timid and difficult to capture. They are usually found in the proximity of detritus which has been washed down into the cave or near bat guano which contains large numbers of invertebrate larvae. The stomach of the male paratype contained three specimens of mayfly nymphs (Ephemeridae). R. D. Burks of the U.S. National Museum has identified them as the genus *Euthyplocia* Eaton (specimens deposited in the USNM). A few broken pieces of *Euthyplocia* tusk were found in the stomach of one of the female paratypes. A specimen of a normally pigmented species of characin (*Piabucina* Valenciennes, determined and now under study by James E. Böhlke, Academy of Natural Sciences, Philadelphia) plus several crustaceans were also taken in the cave with *A. pholeter*.

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THE STATUS OF THE BERMUDA ISH POPULATION OF *JENKINSIA*.—While conducting a survey of the endemic bore fishes of Bermuda, it was found that he Bermuda population of *Jenkinsia* has een described twice, as *Stolephorus viridis* Bean (1912, *Proc. Biol. Soc. Wash. 25:122–*) and as *Jenkinsia bermudana* Rivas (1946, *mith. Misc. Coll. 106(14):1–4*). Nichols 1920, *Proc. Biol. Soc. Wash. 33:63*) and Beebe and Tee-Van (1933, *Zoologica, 13(7): 36*) have pointed out that Bean's species hould be referred to the clupeid genus *enkinsia* rather than to an engraulid genus. They also placed *S. viridis* Bean in the ynonymy of *Dussumieria stolifera* Jordan nd Gilbert, 1884. Beebe and Tee-Van (1928, *Zoologica 10(1):44* and 1933, *op. cit.:136*) laced *stolifera* in the synonymy of *Clupea mprotaenia* Gosse, 1851. In describing *enkinsia bermudana*, Rivas either overlooked Bean's original description or else was unaware that Nichols (*op. cit.*) and Beebe and Tee-Van (1933) had pointed out that Bean's description was of a *Jenkinsia*. I find that the Bermuda population of *Jenkinsia* is indeed different from those present in Florida, the Tortugas, Cuba, Haiti, and Jamaica. Thus, *J. bermudana* should be relegated to the synonymy of *J. viridis*. However, to further complicate the situation, examination of Bean's four cotypes (USNM 74084) showed that there are two species represented. Two specimens are identical with *J. bermudarum* while the other two appear to be the same as the wide-ranging *J. lamprotaenia* (Gosse). The specimens of *J. lamprotaenia* are not in as good a state of preservation as the specimens of *J. viridis*, suggesting that they may have come from elsewhere than Bermuda and somehow became mixed with the two specimens from Bermuda. Unfortunately, Bean did not give the number of specimens that he had other than to say, "Types, from 2 to 2¾ inches long . . . ." Since there is no evidence at present to suggest that there are two species of *Jenkinsia* present in Bermuda, and since it is clear that at least the form with many gillrakers is present, I feel that it is best to restrict the name *Stolephorus viridis* Bean to the two specimens with many gillrakers. Therefore, I designate the larger of the two specimens (45.3 mm standard length) as the lectotype (retaining the catalogue number USNM 74084). It has 10 + 27 = 37 gillrakers (right side, first arch). The paralectotype is 45.0 mm SL and has 11 + 28 = 39 gillrakers (recatalogued as USNM 196658). The other two specimens, which I identify as *Jenkinsia lamprotaenia* (Gosse) are 46.0 and 48.8 mm SL, and have 9 + 23 = 32 and 8 + 22 = 30 gillrakers, respectively (recatalogued as USNM 196659). —Bruce B. Collette, *Ichthyological Laboratory, Bureau of Commercial Fisheries, U. S. National Museum, Washington 25, D. C.*

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THE SWAMP DARTERS OF THE SUBGENUS *HOLOLEPIS* (PISCES, PERCIDAE)

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THE SWAMP DARTERS OF THE SUBGENUS *HOLOLEPIS* (PISCES, PERCIDAE)

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I. Introduction

The object of this paper is to clarify the relationships within and among the darters of the subgenus *Hololepis,* genus *Etheostoma.*

Hubbs and Cannon (1935) thoroughly reviewed the darters of the nominal genera *Hololepis* and *Villora* on the basis of the specimens then available. Extensive collecting in recent years has greatly increased available material and necessitates a modification of some of their conclusions.

Bailey (1951), in Bailey, Winn, and Smith, 1954; and in Bailey and Gosline, 1955 reduced the many nominal genera of darters to three. These are *Percina, Ammocrypta,* and *Etheostoma.* He based this decision on "evidence that the characters employed to define and delimit the groups . . . are highly variable both intraspecifically and interspecifically, are subject to complete overlap from group to group, and are commonly the product of convergent evolution" (Bailey, Winn, and Smith, 1954, page 141). Bailey utilized some of the former genera as subgenera (Bailey and Gosline, 1955: Fig. 1). Although it would be better to have data published before nomenclatorial changes are made, I will follow his use of the name *Hololepis* as a subgenus of *Etheostoma.* However, I can not agree with his implication that the subgenus *Villora* Hubbs and Cannon be made a synonym of *Hololepis* (See Collette and Yerger, 1962). Upon replacing *Etheostoma edwini* in the subgenus *Villora,* the subgenus *Hololepis* constitutes a group of eight forms of small specialized swamp darters. Four of these forms are found in the swamps, lakes, and backwaters of the Coastal Plain, one in the lowlands of the Mississippi Basin, and the other three are limited to the backwaters of Piedmont streams along the Atlantic Coast.

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III. Characters Studied and Their Significance

Counts were made in accordance with the methods outlined by Hubbs and Lagler (1947, 1958) and Hubbs and Cannon (1935) except as modified below. Each group of characters will be discussed to give my interpretation of their relative value in this study.

Lateral-line scales: The total number of lateral-line scales was valuable in distinguishing some species and also in separating races of *E. serriferum.* The number of pored lateral-line scales was especially valuable in the recognition of subspecies of *E. fusiforme.* However, it is subject to developmental variation which made its use somewhat complicated as discussed under development and geographic variation in *E. fusiforme.* The number of unpored lateral-line scales was not studied separately because it is merely an expression of the same factors represented by the total and pored lateral-line scales. Hubbs and Cannon (1935), Bailey (1950), and Bailey and Frey (1951) used the ratio of pored to unpored lateral-line scales. The value of this ratio is negated by the extreme variation of the pored lateral-line scales in *E. fusiforme.* In the other species it merely reflected the number of pored scales and therefore seemed unnecessary.

Scale rows above and below the lateral line: This character was of value in studying the neotenic populations of *E. fusiforme* and is further discussed under geographic variation in *E. fusiforme.* The two species of the subgenus *Villora* have fewer scales below the lateral line than the species of the subgenus *Hololepis,* since the scales are generally larger in *Villora. E. serriferum* has more scales both above and below the lateral line than the other species of the subgenus *Hololepis.*

Fin Rays: The number of first dorsal spines and second dorsal rays was of little taxonomic value. The high number of spines and rays in *E. serriferum* is an indication of its relatively primitive position in the subgenus *Hololepis.* Several populations of *E. fusiforme,* including the Nantucket population named as *fusiforme insulae* by Hubbs and Cannon (1935), had abnormally low dorsal spine counts. The low number of anal rays in *E. zoniferum* helped show its position as a specialized offshoot of *E. gracile* but proved of little value otherwise. The number of anal spines proved significant in the *E. collis* group although Hubbs and Cannon stated that it was consistently two. All *E. collis* and one third of the related *E. saludae,* had only one anal spine. The vast majority of specimens of the other species of *Hololepis* had two anal spines although a few unusual specimens had one or three. There were modal differences between species in the numbers of pectoral rays but this character holds no promise of value in future work. Pelvic elements were I, 5 in all species of *Hololepis,* with only a few specimens having I, 4 or I, 6. For ease of physi

handling, the pectoral and pelvic fins were counted on the right side. Segmented caudal rays were also counted but proved of no systematic value.

Branchiostegal Rays: These were counted on the right side. Virtually all the specimens examined had six branchiostegals, with a few deviations to five or seven.

Cephalic Pores: As pointed out by Hubbs and Cannon (1935), the arrangement and number of pores in the various canals on the head of the species of *Hololepis* are of great systematic importance. The preoperculomandibular pores (operculomandibular pores of Hubbs and Cannon) show strong modes at ten pores for the *E. gracile* group and at nine for the other species of *Hololepis*. *E. serriferum* and *E. saludae* usually have both interorbital pores present while most specimens of the other species of *Hololepis* usually lack these pores. There was no appreciable intra-specific variation in these two canals. The coronal pore is usually present in *Hololepis* but several populations of *Etheostoma fusiforme fusiforme* from the North Carolina Bay Lakes either lack the pore entirely or have it poorly developed. Studies of the relative development of the coronal pore may be of systematic value as mentioned under variation in *E. f. fusiforme*. Development also complicated the use of the supratemporal canal as a systematic character. Most *E. fusiforme, serriferum,* and *gracile* had this canal complete with the left and right branches uniting in a median pore at the occiput. Individuals of the *E. collis* group were about equally divided between complete and incomplete supratemporal canals, a feature which I consider specialized. The general picture of the growth of this canal is discussed under development in section IV. The infraorbital pores showed a number of different patterns which were modally species specific. *E. serriferum* (six pores) and *E. gracile* (eight pores) have complete infraorbital canals. The other species of *Hololepis* have incomplete canals with the anterior portion of the canal separated from the posterior portion. The northern subspecies of *E. fusiforme* has 2 + 3 (posterior plus anterior portion) pores while the southern subspecies has 1 + 3 pores with many interesting variations which are discussed fully under geographic variation in *E. fusiforme*. For ease of handling, pore counts of the infraorbital and preoperculomandibular canals were made on the right side of the specimens.

Condition of the Preopercle: The right side of the preopercle was examined for serrae. The condition was recorded as S (serrate), PS (partially serrate, or E (entire or non-serrate). Hubbs and Cannon (1935) stated that *E. serriferum* could be distinguished from the other species of *Hololepis* by the presence of serrations on its preopercle. The presence of a few preopercular serrations in some specimens of *Etheostoma fusiforme barratti* led some workers to believe that these specimens might represent hybrids between *E. serriferum* and *E. f. barratti*. Bailey (1950) used the presence of many preopercular serrations in specimens of *barratti* from the French Broad River as a diagnostic character of his *Hololepis barratti appalachia*. As discussed under geographic variation in *E. fusiforme*, the presence of these serrations varies in a roughly clinal manner, the percentage of individuals with them increasing from north to south.

Squamation: The parietal, interorbital, breast, opercle, preopercle, and nape were examined for the development of squamation. The number of scales was counted in the interorbital region while the area covered and the type of scales were recorded in the other areas. The interorbital region is defined as the area between the orbits anterior to the nares and posterior to a line between the eyes at the level of the coronal pore, where the parietal area begins. In *E. serriferum* and *E. fusiforme*, the skin with contained scales was dissected off and the scales were removed and counted under magnification. The scales were frequently small, imbedded, and sometimes in a number of vertical layers, making counting difficult. This scale count allowed the separation of races in *E. serriferum* and subspecies in *E. fusiforme*. As with the other squamation examinations, only adult specimens were used since these regions are less scaled or naked in juveniles.

The area covered by scales in the other regions was estimated to the nearest 10% (similar to the method used by Lagler and Bailey, 1947). The amount of imbedding was recorded: X (posterior edges of the scales completely exposed), PX (scales with

their posterior margins partly exposed), or I (scales completely imbedded in the epidermis). The type of ctenoid or cycloid scales was recorded: T (ctenoid scales with at least one spine on the posterior margin), or C (cycloid scales, completely lacking ctenii). When two conditions were present in a given region, both symbols were recorded, separated by a diagonal. Thus the formula for a region might be: 50% I/PX-C/T meaning half the region was covered by scales of which some were imbedded and others partly exposed and some were cycloid and others ctenoid. These symbols are used in the squamation tables to save space.

The parietal region is the area from the interorbital region posterior to the supratemporal canal bounded laterally by the light line that runs just above the lateral canal. This definition excludes the single row of scales usually present beween the lateral canal and the light line. The nape region is a roughly triangular area with its base at the supratemporal canal and its apex at the origin of the first dorsal fin. The breast region is the triangular area starting on a line just anterior to the origin of the pelvic fins and extending forward to immediately behind the union of the gill covers. The opercular and preopercular regions include the surfaces of those bones and were examined on the right side.

Breeding Tubercles: Specimens were examined for breeding tubercles while counts were being made. The specimens showing maximum development of tubercles were selected for study. Breeding males of all species of the subgenus *Hololepis* have tubercles on the rays of the anal and pelvic fins, although the number and exact distribution of the tubercles varies between and within species. In the descriptions of breeding tubercles of each species, the rays of the anal and pelvic fins are numbered, starting behind the spines. Tubercle distributions of several species are pictured (Fig. 1).

The use of breeding tubercles as a systematic character in darters has been totally neglected. There are literature reports of breeding tubercles in nine species of darters while I have found them in more than 40 species in a study that has not been completed. As in the Cyprinidae and Catostomidae, tubercle patterns characterize some taxonomic groups. Two instances of tubercle pattern pertinent to this study are: (1) th subgenus *Villora* differs from the subgenu *Hololepis* in lacking breeding tubercles; an (2) the close relationship of *E. gracile* an *E. zoniferum* is demonstrated by their bein the only species of *Hololepis* to have acces sory breeding tubercles on their lower jaw

Genital Papillae: As pointed out by Hubb and Cannon (1935), breeding female *E serriferum* possess flattened and bilobe genital papillae as contrary to the conica pointed genital papillae present in the othe species of the subgenus *Hololepis.* As note under the subgeneric diagnosis, *Hololep* can be distinguished from *Villora* by it elongate genital papilla. Drawings of th different types of genital papillae are pre sented (Fig. 1) to supplement text descrip tions.

Sex: Dissections were made on a rela tively few specimens to verify external se determinations. Thereafter sex was dete mined externally by the enlargement of th female genital papilla and by the more pig mented venter and dorsal, anal, and pelvi fins of the males. These characters allowe the determination of sex in specimens a small as 20 mm. Smaller specimens wer listed as juveniles.

Measurements: Due to the great abun dance of other characters, and to the state ment by Hubbs and Cannon (1935) abou the slight value of morphometrics in *Hol lepis,* only the standard length was take Standard length is particularly important i *Hololepis* because variation in several cha acters is correlated with specimen size (Se tion IV, development).

Range: Figures 3, 5, and 8 show the di tribution of each form (based upon spec mens personally examined) in relation t the Fall Line which is important in lim iting the distribution of all the species o the subgenus *Hololepis,* except *E. gracil* When several collections were available fro a small area, all were not plotted. Collectio of all specimens examined are given by m seum number, county, and state for th various drainages. More complete locali data are given for rare forms, range exte sions, or other reasons. Complete data f most collections examined may be found my thesis (Collette, 1960).

Ecology and Habits: To become mo familiar with *Hololepis* I have made seve

hundred collections in 21 of the 27 states where they are found. I have maintained *E. serriferum, gracile, fusiforme fusiforme,* and *f. barratti* in aquaria for varying lengths of time to obtain some understanding of their feeding, courtship, and other behavior.

Synonymies: I have attempted to examine all references that mention any of the *Hololepis* in any manner. The synonymies under each form include all references since the publication of Hubbs and Cannon's (1935) revision and all significant ones prior to that time.

Sampling: I made complete counts on

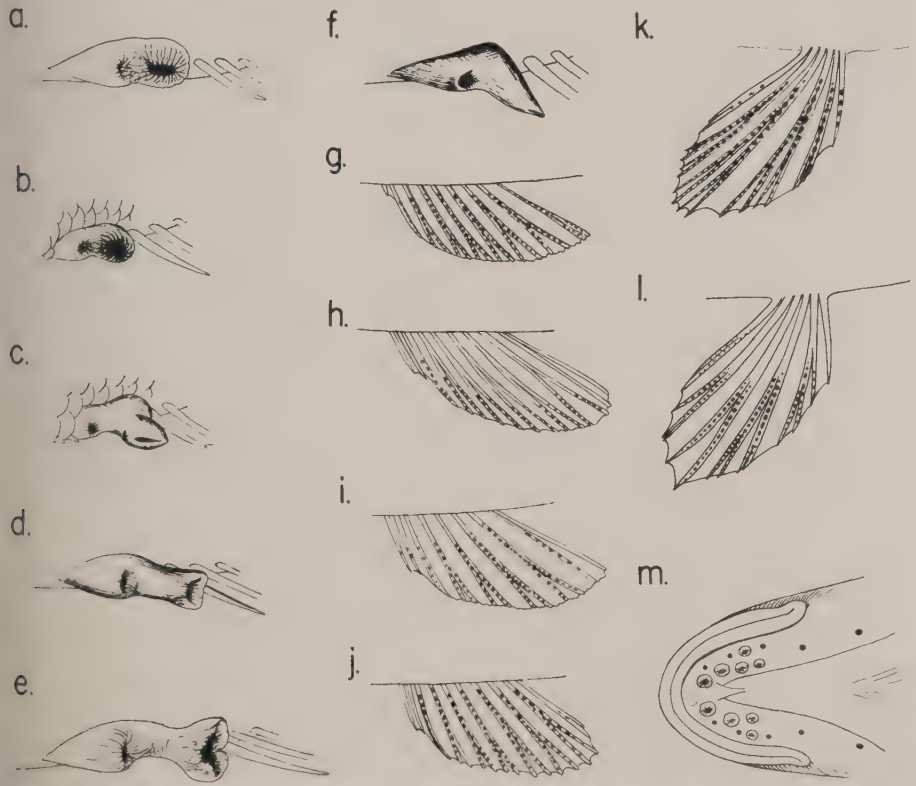


Figure. 1. Genital papillae and breeding tubercles in some of the species of the subgenera *Hololepis* and *Villora*. **a**. *Etheostoma edwini*. Genital papilla of 38.1 mm female taken on March 26. (CU 29754, Ga., Apalachicola dr.) **b**. *Etheostoma edwini*. Genital papilla of 38.5 mm female taken on March 26. (CU 29754, Ga., Apalachicola dr.) **c**. *Etheostoma gracile*. Genital papilla of 40.4 mm female taken on March 7. (TNHC 2750, Tex. San Jacinto dr.) **d**. *Etheostoma serriferum*. Genital papilla of 42.3 mm female taken on March 24. (CU 29976, Va., Chowan dr.) **e**. *Etheostoma serriferum*. Genital papilla of 56.6 mm female taken on March 31. (CU 15614, N. C., Cape Fear dr. **f**. *Etheostoma f. fusiforme*. Genital papilla of 37.0 mm female taken on April 19. (CU 31847, N. Y., L. Yaphank). **g**. *Etheostoma c. collis*. Breeding tubercles on the anal fin of 34.4 mm male taken on March 22. (CU 11988, N. C., Yadkin-Pee Dee dr.) **h**. *Etheostoma gracile*. Breeding tubercles on the anal fin of 36.4 mm male taken on March 8. (TNHC 2575, Tex., Neches or Trinity dr.) **i**. *Etheostoma serriferum*. Breeding tubercles on the anal fin of 36.0 mm male taken on March 23. (CU 30122, S. C., Pee Dee dr.) **j**. *Etheostoma f. fusiforme*. Breeding tubercles on the anal fin of 36.0 mm male taken on April 19. (CU 31847, N. Y., Lake Yaphank) **k**. *Etheostoma gracile*. Breeding tubercles on the right pelvic fin of 37.2 mm male taken on April 15. (OAM 4192, Okla., Red dr.) **l**. *Etheostoma serriferum*. Breeding tubercles on the right pelvic fin of 43.9 mm male taken on March 23. (CU 30122, S. C., Pee Dee dr.) **m**. *Etheostoma gracile*. Breeding tubercles on the chin of 37.2 mm male taken on April 15. (OAM 4192, Okla., Red dr.) **(Drawings by Rudolph J. Miller)**

virtually all the specimens at the beginning of this study. In a few cases, where a large series was available from a single locality, some specimens were omitted. As the study progressed and certain characters were shown to be either constant or to vary within a narrow range with no significant geographical variation, counts were made only on part of the available specimens. Thus, fewer counts were made on pectoral and pelvic fin rays, branchiostegals, segmented caudal rays, and coronal pore development. The number of specimens examined for squamation is less than for meristic counts because only adult specimens could be used (Section IV, development).

Presentation of Results: Only characters that are virtually constant for the subgenus are given in the subgeneric diagnosis. Counts that show significant interspecific, but relatively little intraspecific variation are presented in the species comparisons tables (Tables 38-49). The two species of the subgenus *Villora* are also included in these tables for comparison. Characters showing geographic variation are presented in tables by species or species groups. In these tables populations are listed down the page in geographic order from north to south along the Atlantic Coast and from east to west along the Gulf Coast. The Mississippi River was divided into sections and subsections for the analysis of variation in *Etheostoma gracile.* A relatively large number of tables is presented so that the reader may see clearly why certain taxonomic decisions were made and, more importantly, so that the entire picture of variation in a particular species can be seen.

IV. Causes of Variation

In any variational study, it is necessary to examine the types of variation present and to consider the factors that may be involved in causing them. While all types of variation are interesting from an evolutionary point of view, it is desirable to eliminate non-genetic sources of variation for taxonomic purposes. The following sections consider variation due to asymmetry, sexual dimorphism, year classes and development.

Left and Right Sides: As has frequently been done by ichthyologists, Hubbs and Cannon (1935) in their revision of *Hololepis* sometimes made counts on the left side, sometimes on the right side, and sometimes on both sides. Nowhere do they mention why they feel this is justified or even the fact that they are doing it. However, by comparing the number of specimens they examined with the number of counts of median and bilateral structures, I found that for median counts, they gave counts for up to the number of specimens examined while for bilateral counts, they gave up to twice as many counts as specimens examined. I do not feel that this is proper for two reasons. Firstly, as stated clearly by Hubbs and Hubbs (1945, page 300): "Since many superficial as well as internal characters are often more or less different on the two sides it is obviously a wise policy in systematic studies to count or measure given characters consistently on one side, or to study both sides." Secondly, even if there are no differences between sides, use of both sides can lead to misinterpretations unless the two sides are independent, which seems quite unlikely.

In order to interpret some of Hubbs and Cannon's conclusions, the possibility of left-right correlation was examined using collections of *Etheostoma f. fusiforme* made in two Long Island, N. Y. ponds. Pored and total lateral-line scales were counted on both sides of these fish and the left side was plotted against the right (Collette, 1960, Figs. 1-2). With regard to the pored lateral line scales, the percent of individuals having the same count on each side was 23%, a difference of plus or minus one or two scales 30 and 34%, and a difference of greater than two scales 8 and 4 %. For the total lateral-line scales, the percentages were 19 % no difference, 24 and 25 % with a difference of plus or minus one or two scales, and 11 and 11 % with a difference greater than two scales between sides. This means that if both sides were counted and put into a single frequency distribution the sample size would appear to be doubled with the probability that the range would not be increased nearly as much as if the sample size had really been doubled. In the case of three of Hubbs and Cannon's subspecies of *E. fusiforme* (*f. insulae* from Nantucket Island, *f. metaegadi* from Cape Cod and *f. atraquae* from the Potomac River) each of which is based upon a single sample the supposed subspecies appears more hom-

geneous and therefore more different from other populations of the species than is really the case. (The validity of these forms are discussed at length under geographic variation in *E. fusiforme.*)

Sexual Dimorphism and Year Class Variation: The variation due to sexual dimorphism and year class differences is frequently not considered in taxonomic studies. Inspection of the data showed that such variation could be significant only in the number of lateral-line scales. Table 1 shows comparisons between males and females in the number of pored and total lateral-line scales. Samples for single localities were used for all but one species. A sufficiently large sample of *E. saludae* was not available, so it was necessary to lump all the samples. This should not introduce error due to geographic variation because this species has a restricted range. No significant differences are apparent between the sexes in these characters (Table 1).

Little material of different year classes from single localities is available. Three year classes of *E. collis collis* from the Yadkin River and year classes of *E. fusiforme fusiforme* from two of the North Carolina Bay Lakes and a Long Island pond were employed in comparisons. The relative contributions of sexual dimorphism and year class variation were analyzed by the use of an R X 2 table with disproportionate subclass numbers (Snedecor, 1956). The preliminary analyses of variance show that there is no significant variation due to sexual dimorphism or year class variation for *E. c. collis* ($F = 1.782$ for pored lateral-line scales and 1.636 for total) or for *E. f. fusiforme* from Lake Yaphank ($F = 0.938$ and 1.027) and Jones Lake ($F = 0.931$ and 1.834). There are also no significant differences in pored lateral-line scales between different year classes in White Lake ($F=2.219$). There is a significant difference at the 99% level ($F = 4.116$) in total lateral-line scales (Table 2). To determine whether this was due to sexual dimorphism or year class variation the analysis was completed. Table 2 presents the means for year classes and sexes, the preliminary analysis, and the completed analysis. The difference between sexes is significant at the 95% level. This is not deemed important taxonomically because the total number of lateral-line scales in *E. fusiforme* is not a significant character in analyzing geographic variation.

Development: The development of squa-

TABLE 1.
Variation between sexes in pored and total lateral-line scales in Etheostoma (Hololepis) species

Species	*serriferum*		*gracile*		*f. barratti*	
Locality	Pee Dee		Red		Savannah	
	Pored Lateral-line Scales					
Sex	M	F	M	F	M	F
N	23	22	21	26	33	44
Range	29-38	28-39	17-25	15-23	20-37	18-34
$\bar{x}$	32.8	34.9	20.0	18.3	26.3	25.0
	Total Lateral-line Scales					
N	24	23	21	26	33	47
Range	50-60	48-62	45-53	42-50	51-62	50-63
$\bar{x}$	54.1	54.4	48.1	46.9	56.2	54.8

Species	*fusiforme fusiforme*				*saludae*		*c. collis*	
Locality	Chowan		Chesapeake		All specimens		Yadkin	
	Pored Lateral-line Scales							
Sex	M	F	M	F	M	F	M	F
N	31	54	39	21	26	56	17	14
Range	11-17	11-19	13-23	14-24	11-23	5-29	9-23	11-24
$\bar{x}$	14.2	14.6	17.9	18.0	17.2	16.7	15.5	15.5
	Total Lateral-line Scales							
N	31	56	39	23	29	54	17	13
Range	41-54	42-54	46-58	48-58	36-47	37-50	42-49	40-47
$\bar{x}$	48.3	48.4	51.6	51.2	41.2	42.1	44.8	44.1

TABLE 2.
Variation of total lateral-line scales between year classes and sexes in Etheostoma f. fusiforme from White Lake, N. C.

Year	n_1	F_1	n_2	F_2	W	D	WD
	Male		Female				
1947	37	49.51	34	50.06	17.7183	0.55	9.745
1958	11	48.64	37	49.38	8.4792	0.74	6.274
1959	13	48.54	31	51.32	9.1591	2.78	25.462
	61		102				41.482

Preliminary Analysis of Variance of Original Data

Source of Variation	d.f.	Sum of Squares	Mean Square	F
Treatments	5	119.341	23.868	4.116**
Years	2	38.408	19.204	
Sexes	1	41.975	41.975	
Error	157	872.377	5.556	
Total	162	991.718		

Completed Analysis

Sexes	1	48.669	24.334	4.380*
Years	2	18.039	9.020	1.623 N.S
Interaction	2	32.112	16.056	2.890 N.S
Error	157	872.377	5.556	
Total	162	991.718		

(Analysis of variance with an R x 2 table and disproportionate subclass numbers, is significant at the 95% level, ** at the 99% level)*

mation, pored lateral-line scales, supratemporal canal, infraorbital canal, and coronal pore proved to be important in studying variation in *Hololepis*. This was especially true in understanding the extreme variation in number of pored lateral-line scales in *Etheostoma fusiforme fusiforme* from the North Carolina Bay Lakes and in *E. f. barratti* from Crystal Lake, Georgia. While specific information on development will be found under each species, I think it will be of value to briefly state the over-all pattern of development as I understand it.

Scales first appear on the caudal peduncle at the base of the caudal fin when the fish are about 15 mm SL. They then extend forward along the lateral line and spread dorsally and ventrally from the lateral line. The breast, belly, nape and head are the last regions to develop scales. Areas that have ctenoid scales in the adult develop scales faster than areas that have imbedded cycloid scales in the adult. The pattern of scale development is thus very similar to that given for *Micropterus dolomieui* (Everhart, 1949), *Pomoxis nigromaculatus* (Ward and Leonard, 1954), *Perca flavescens* (Pycha and Smith, 1955), etc.

Pored lateral-line scales do not develop until after the body squamation is virtually complete. Two lateral ridges form on eac of the most anterior scales in the lateral lin These ridges grow higher and then mee over the middle of the scale to form th pore. The number of pored scales increas rapidly through 5-10 mm until the definitiv number is reached by about 25 mm S (Figs. 11, 12). Populations of some speci (*e.g., E. fusiforme*) are neotenic in retainin a reduced number of pored scales.

The supratemporal canal is incomplete juveniles of all species of *Hololepis*, and b comes complete in adults of most speci by the two branches growing together lea ing a median pore as a vestige of the former separation. An incomplete supr temporal canal may be characteristic populations of a species, an entire speci or larger categories. The infraorbital can grows posteriorly from its origin behind t nostril and anteriorly from its junction wi the lateral canal. In some species the can is interrupted while in others the two po tions grow together to form a comple canal. The coronal pore grows posterio from the connection between the sup orbital canals. Specimens sufficiently sm were not available for a study of the d velopment of the other canals.

It is apparent that one of the features

volution in the darters is the relative completeness of development of some of the characters mentioned above. Independently in many different lines of darters, various primitive characters have been repressed. Thus in the subgenus *Nothonotus, E. tippecanoe* stands out as the most advanced species being the smallest in size, having the belly squamation reduced, and having an incomplete lateral line. *Microperca,* the most advanced subgenus of *Etheostoma,* shows the effects of incomplete development in almost all characters: dorsal spines, anal rays, lateral-line scales, pored lateral-line scales, size, etc. The three species of *Microperca* can be ranked phylogenetically by the amount of development of various characters: the most primitive (*E. proeliare*) has 2-7 pored scales and the preopercle and opercle are scaly. The two more advanced species lack pored scales and scales in those areas. *E. fonticola,* the most advanced species, has the anal spines reduced to one. The same type of situation is shown in *Hololepis* in section VI, evolutionary relationships.

V. Subgeneric Diagnosis
Hololepis Agassiz, 1863

Hololepis Agassiz, in Putnam, 1863: 4 (type species *Boleosoma barratti* Holbrook, 1855, by subsequent designation of Jordan and Gilbert, 1877: 93).

Copelandellus Jordan and Evermann,1896: 1100 (type species *Poecilichthys quiescens* Jordan, 1884, by original designation).

Lateral line arched upward anteriorly and always incomplete; pored lateral-line scales 0 to 45; unpored 12 to 52; total 35 to 66; infraorbital canal complete or incomplete; interorbital pores 0, 1, or 2; supratemporal canal usually complete in adults; coronal pore usually present; preoperculomandibular pores 6 to 12, usually 9 or 10; vomer and palatine toothed; preopercle entire, partially serrate, or serrate, entire in most species; branchiostegal membranes narrowly conjoined; branchiostegal rays usually 6; opercle, preopercle, breast, nape, interorbital, and parietal regions naked to fully covered with embedded cycloid to exposed ctenoid scales; belly covered at least in part with unspecialized cycloid or ctenoid scales; flesh opaque; body rather compressed and elongate to somewhat stocky; vertebrae 35 to 41; premaxillary frenum broad; first dorsal fin moderately high, with 7 to 13 spines which lack thickened, fleshy tips; anal spines 2 in most species, the first somewhat shorter and thicker than the second, the second equal to one-half to three-quarters of the length of the first anal ray; pelvic fins closely approximated, separated by one-half to three-quarters of the fin base; pectoral rays 10 to 15; second dorsal rays 8 to 17; anal rays 4 to 10; genital papilla of breeding female modified into an elongate and either cylindrical or somewhat flattened and bilobed tube; breeding tubercles present in breeding males on the anal fin rays and the undersides of the pelvic fin rays; maximum size of males equal to or less than that of females; habitat slow-moving waters such as lakes, swamps, and the backwaters of streams.

The subgenus *Hololepis* appears to be most closely related to the subgenus *Microperca,* and to some species of *Oligocephalus* (e.g., *Etheostoma exile*). The subgenus *Hololepis* is distinguished from *Microperca* by a more complete lateral line; more lateral-line scales; the presence of a premaxillary frenum; and the absence of the peculiar flap on the pelvic fins of breeding male *Microperca. Etheostoma* (*Hololepis*) *collis* and *saludae* are the species of *Hololepis* that resemble most the species of *Microperca* in body shape, coloration, male breeding pigmentation, reduced number of pored lateral-line scales, and having forms with both one and two anal spines. *Microperca,* while distinguishable as a subgenus, appears to be further along on the same phyletic line as *Hololepis.*

From the subgenus *Villora, Hololepis* is distinguished by a more highly arched and less complete lateral line; an elongate genital papilla in breeding females as contrasted with the low tube crowned with villi in *Villora;* presence of nuptial tubercles on the pelvic and anal fins of breeding males; lack of a strongly developed black humeral spot; maximum size of males less than that of females; and a habitat of slow, muddy waters (see also diagnosis of *Villora* in Collette and Yerger, 1962).

Etheostoma (*Oligocephalus*) *exile* shows a number of similarities to the species of the subgenus *Hololepis.* These include compressed body form; arching of the lateral line, incomplete development of the lateral

line, and slow water habitat. On the other hand, male *E. exile* have much more brilliant breeding colors than do any of the species of the subgenus *Hololepis* and apparently lack breeding tubercles.

I think that the phyletic line that goes from *Hololepis* through *E. collis* and *E. saludae,* culminating in *Microperca,* probably has its origin somewhere in *Oligocephalus,* perhaps near *E. exile*.

VI. Evolutionary Relationships in *Hololepis*

The characters used to delimit subspecies, species, species groups, subgenera, and genera in the darters show many cases of convergent and divergent evolution as noted by Bailey (in Bailey, Winn and Smith, 1954, p. 141). Characters which can be considered as generalized in the darters include: serrate preopercle; conical genital papilla; deep compressed body; relatively large body size; gill membranes separate; most areas of the body covered with ctenoid scales; lateral line complete and not arched; ten preoperculomandibular pores; infraorbital canal complete with eight pores; supratemporal canal complete; interorbital pores present; two anal spines; 41-45 vertebrae; sexual dimorphism and sex recognition weakly developed; females equal to or larger in size than males; non-territorial; eggs scattered over wide area; no parental care; habitat of large streams (modified from Hubbs and Cannon, 1935; Bailey and Gosline, 1955; Winn, 1958; etc.).

Of the species in the subgenus *Hololepis, E. serriferum* is the most primitive in virtually all characters. It is the largest species of the subgenus, has a serrate preopercle, interorbital pores present, infraorbital canal complete (although pores reduced to six); and has a more complete lateral line, more dorsal spines and rays, more scales below the lateral line, more lateral-line scales, and a scalier nape, parietal, and interorbital than the other *Hololepis.* Its only real specialization is the bilobed genital papilla of the breeding female although it also shows a reduction in the number of preoperculomandibular pores (to nine) and infraorbital pores.

Etheostoma gracile and *E. zoniferum* share a number of characters which indicate that they are closely related. These include ten preoperculomandibular pores; interorbital pores absent; naked breast, pari tal, and interorbital; green vertical bars c the sides in life; rows of red spots in th dorsal fins of breeding males; the presen of accessory breeding tubercles on the chi of breeding males; and territorial behavio There is a combination of primitive cha acters (ten POM pores) with specialize ones (INT absent, breast and nape nake territorial behavior). Most of the characte that differentiate *E. zoniferum* from *E. gr cile* indicate that it is an offshoot of *gracile*. This is especially true of the mo important differentiating character which the incomplete infraorbital canal in *zon ferum. E. zoniferum* also shows a reductio in the number of anal rays, scales above an below the lateral line, pored lateral-li scales, squamation of the breast and pr opercle, and usually has the supratempor canal incomplete. Only in the more exte sive opercular squamation does *zoniferu* appear less specialized than *gracile.* A parently, *zoniferum* differentiated from *gr cile* after isolation in the Alabama and Tom bigbee Rivers, east of the range of the wid spread *gracile.*

Etheostoma fusiforme is the most wid spread species of *Hololepis.* It shows a fe more advanced characters over the *E. graci* group such as having the preoperculoman bular pores reduced to nine, and the infr orbital canal interrupted with 1 + 3 or 2 + 3 pores. In several other characters it slightly more primitive than the *E. graci* group. It has slightly more lateral-line scal and vertebrae; scalier interorbital, pariet and breast; the occurrence of individu with partially serrate preopercles; and t ritoriality is absent. In all respects but o *E. fusiforme fusiforme* is clearly a speci ized offshoot of *E. f. barratti.* It has few pored lateral-line scales, a lower percenta of individuals with partially serrate preop cles, and a reduced squamation, especia in the interorbital and parietal regions. *E barratti,* however, has a higher percenta of individuals with 1 + 3 infraorbital po while *f. fusiforme* usually has 2 + 3. So of these characters show clinal variatio The extent of squamation and the perce age of individuals with partially serrate p opercles increases toward the south. Ot characters have a much more complex v

on as discussed at length under geographic riation in *E. fusiforme.*

The *Etheostoma collis* group is the most ecialized in the subgenus. Here the pored eral-line scales are further reduced in mber; the supratemporal canal is fre-ently incomplete; there are fewer verte-ae, fewer lateral-line scales; and one anal ine is frequently absent. The three forms this group have deserted the lowland bitat characteristic of the other *Hololepis* r backwaters of Atlantic Piedmont streams. *saludae* is clearly the most primitive of e three since it retains the interorbital ores and only about a third of the speci-ens have the anal spines reduced to one. *saludae* and *E. collis lepidinion* are scalier an *E. c. collis,* especially in the nape and east regions. *Etheostoma c. collis* is the ost specialized *Hololepis.* It has one anal ine; no interorbital pores; infraorbital + 3; breast, nape, parietal, and interorbital ked. There is still some doubt in my mind to the taxonomic categories to use for the *collis* group. There may be one species ith three subspecies, three species, or two ecies with the Roanoke-Neuse River form subspecies of *E. collis.* In two respects, *saludae* is intermediate between *E. c. col-* and *E. c. lepidinion:* number of infra-bital pores and squamation of the nape. n the basis of one anal spine and the ab-nce of interorbital pores, I have decided consider the Roanoke-Neuse and Pee ee-Catawba forms as conspecific, thus aking *lepidinion* a subspecies of *E. collis.* Thus it is apparent that the species of *lololepis* form four species groups, and within each of these groups there are specialized and generalized characters so that these four lines are offshoots of some more primitive stock. The intra-group relationships are clearer: *E. serriferum* is the most primitive *Hololepis; E. zoniferum* is a specialized derivative of *E. gracile; E. fusiforme fusiforme* has undergone a reduction in squamation and other characters in developing from *E. f. barratti; E. saludae* has given rise to *E. collis lepidinion* which has subsequently differentiated into *E. collis collis,* probably the most advanced of the *Hololepis.*

VIII. Species Accounts

Etheostoma serriferum (Hubbs and Cannon)

Boleichthys fusiformis—Driver, 1942:285 (range in key partly *serriferum*).

Hololepis serrifer—Hubbs and Cannon, 1935:31-36, pl. I, (original description); Fowler, 1945:40, 139 (N.C.), 196 (S.C.); Freeman, 1952a:37 (Congaree and Wateree r., Richland Co., S.C.); Bailey and Frey, 1951:191, 203 (Ellis L., N.C.); Anderson and Freeman, 1957: 106 (Congaree R., S.C.); Randall, 1958:342 (Catawba-Wateree R., S.C.).

Etheostoma serriferum—Bailey and Gosline, 1955:20, 44 (number of vertebrae); Eddy, 1957:219-220; Moore, 1957:197; Collette, 1961:2051.

Misidentifications—Etheostoma fusiforme barratti as *Hololepis serrifer,* Fowler, 1945: 252 (Savannah R., Ga.).

Types—Holotype, UMMZ 107053; 52 mm male; N.C., Wake Co., Buffalo Cr.;

VII. Key to the Species and Subspecies of the Subgenus *HOLOLEPIS*

Infraorbital canal complete	2
Infraorbital canal interrupted	3
Preopercle strongly serrate; infraorbital pores 6	*E. serriferum*
Preopercle entire; infraorbital pores 8	*E. gracile*
Preoperculomandibular pores 10; interorbital pores absent; anal spines 2	*E. zoniferum*
Preoperculomandibular pores 9; interorbital pores 0, 1, or 2; anal spines 1 or 2	4
Interorbital pores absent; breast squamation 100%; interorbital with 0-37 scales	*E. fusiforme* 5
Interorbital pores 0, 1, or 2; breast squamation 0-80%; interorbital naked	6
Interorbital with 0-12 scales, usually 0-4; infraorbital pores usually (80%) 2+3	*E. fusiforme fusiforme*
Interorbital with 1-36 scales, usually 5-20; infraorbital pores usually (70%) 1+3	*E. fusiforme barratti*
Anal spines 1 or 2; interorbital pores present	*E. saludae*
Anal spines 1; interorbital pores usually absent	*E. collis* 7
Breast squamation 10-80%; nape squamation 70-100%; infraorbital pores usually 1+4	*E. collis* LEPIDINION
Breast naked; nape squamation 0-40%; infraorbital pores usually 1+3	*E. collis collis*

Wendell; Brimley and Harris; Nov. 19, 1925. Paratypes: all other specimens examined by Hubbs and Cannon (1935:31-33).

Diagnosis—Differs from the other species of *Hololepis* by having a completely serrate preopercle. The female has a flattened bilobed genital papilla. There are two intense black spots at the base of the caudal with a pair of fainter spots above and below them. *E. serriferum* has more second dorsal rays (mode: 14, $\bar{x}$: 13.6) than other species of *Hololepis* (modes: 11 or 12, $\bar{x}$: 10.6-12.4) and more scales below the lateral line (mode: 12, $\bar{x}$: 11.8) than other species of *Hololepis* (mode: 8 or 9, $\bar{x}$: 8.1-8.9). Both interorbital pores are usually present as in *E. saludae*. Parietal region completely covered with scales. Infraorbital canal complete as in *E. zoniferum* but usually with only six pores instead of eight. Maximum size: males—52.1 mm (CU 29981, Roanoke R.) and females—57.4 (CU 35059, Santee R.).

Coloration—The first dorsal fin of the female is clear or has small melanophores concentrated on or near the spines and between their bases. The second dorsal fin is indistinctly barred and may have pigment at the base of the membranes. The anal either lacks pigment or has melanophores concentrated on the rays in groups, which give a barred appearance. Both pector and pelvic fins are clear or have melan phores outlining the rays. The caudal barred; pigment is also present on the prox mal portion of the membranes in som specimens. The belly and breast are usuall immaculate, but sometimes have a fe scattered large melanophores. The cheek ha a few large melanophores. All four orbit bars are present but not especially prom nent; the supraorbital extends onto the ey The pored portion of the lateral line appea as a narrow light line. A pair of intens black spots occur above and below the mi caudal base. Faint spots are found at bot the dorsal and ventral bases of the caud in most specimens. Black lateral blotch are usually fused into a band below the la eral line. Some specimens have uniform tan sides without lateral blotches. Dors saddles and blotches are absent. The genit papilla is usually immaculate but may hav some pigment posteriorly. Figure 2 show a female.

The cheek and first dorsal fin of the no breeding male are colored like those of t female but have a few more melanophore The anal fin has scattered melanophores o the membranes and rays; there are few on the rays. The belly and breast vary fro

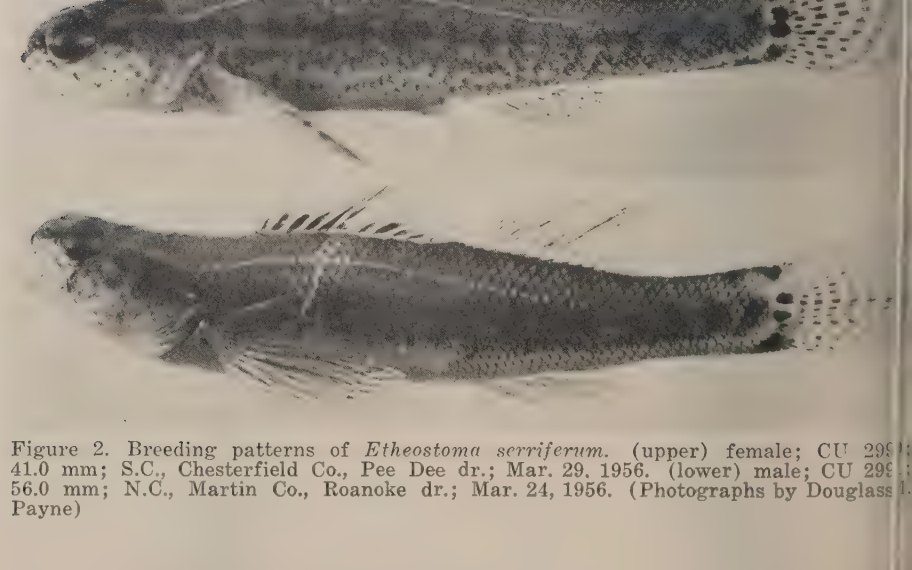


Figure 2. Breeding patterns of *Etheostoma serriferum*. (upper) female; CU 29 41.0 mm; S.C., Chesterfield Co., Pee Dee dr.; Mar. 29, 1956. (lower) male; CU 29 56.0 mm; N.C., Martin Co., Roanoke dr.; Mar. 24, 1956. (Photographs by Douglass Payne)

maculate to an overall sprinkling of small elanophores. The orbital bars are more ominent in some non-breeding males than females. The narrow light line along e pored portion of the lateral line appears ore prominent in the male because of the rker sides. Melanophores usually form a nd that encircles the base of the genital pilla.

In the breeding male the pectoral and udal fins, basi-caudal spots, sides, dorsal rface, and the genital papilla are similar the non-breeding male; other areas are rker. The basal portion of the first dor- l fin is almost solid black. A narrow clear nd borders the membranes between the st spines. The membranes of the second rsal fin are covered with large melana- hores which do not form rectangular lotches as they do in *E. saludae* and *collis.* he anal and pelvic fins and the belly and reast are uniformly covered with small elanophores. The suborbital bars are less rominent than in the female because the eeks are darker. The light line along the ored portion of the lateral line is inter- upted by some pigment on the distal parts f the scales. The breeding pattern of a ale is shown in Figure 2. Hubbs and Can- on (1935:36) used Jordan's (1890:120) escription for life colors. The description entions red on various areas of the body hich does not at all agree with my ob- rvations.

Breeding Tubercles—Breeding tubercles re present on the anal rays and the lower rface of the pelvic rays. In a 40.2 mm ale taken on March 24-25 (UG 152) rom the Ogeechee River, breeding tuber- les occur on the distal one third of anal ays one through four, the distal quarter of elvic rays one through three, and the distal ghth of pelvic ray number four. In a male ken on March 30 (CU 15636, #2) from he Pee Dee River, tubercles are present on he distal two thirds of the anal rays, mostly n the main branches, and on the distal one hird of the pelvic rays, mostly on the naller branches. At maximum develop- ent the tubercles are moderately large. igure 1l shows their distribution on the elvic fin of a 43.9 mm male taken on March 23 (CU 30122) and Figure 1i shows he tubercles on the anal fin of a 36.0 mm ale from the same collection.

Genital Papilla—The other species of the subgenus *Hololepis* have a moderately elongate tube with a sharp or blunt end, but in *E. serriferum* the females have the tip of the tube flattened and bilobed. The long axis of the opening of the papilla is perpendicular to the papilla, while in other species of *Hololepis* the opening is parallel to the papilla. Figure 1d shows the papilla of a female taken on March 24 from the Chowan River (CU 29976). Figure 1e shows the most extreme development of a papilla noted in *E. serriferum*: a female (56.6 mm) from the Cape Fear River taken on March 31 (CU 15614).

Habitat—E. serriferum prefers slightly more open, better oxygenated, and less sluggish waters than most species of *Hololepis.* In collections containing both *E. fusiforme* and *E. serriferum,* the former species is limited to the backwaters of streams, while the latter is usually found in clumps of weeds in the middle of the stream. The larger, less compressed body of *E. serriferum* perhaps permits this species to resist the force of the current more efficiently than *E. fusiforme.* However, both species have been taken together in some lakes (*e.g.,* Ellis Lake, N.C.).

At 16 localities where I collected *E. serriferum,* the current was slow (5), slow to moderate (3), and moderate (8); the bottom composed partly of sand in 13 collections, mud and/or silt (8), detritus (4), and clay (3); the vegetation ranged from sparse emergents along the shore to dense stands of aquatic plants (in Ellis Lake); the water was usually clear and stained brown; the width of the streams varied from 5 to 30 feet (also taken in two lakes); and the shore was wooded or open.

Species Associates—Examination of my field notes for 16 North Carolina collections which contained *E. serriferum* shows the following to be frequent associates (number of collections present with *serriferum* given in parentheses): *Aphredoderus sayanus* (11); *Etheostoma f. fusiforme* or *f. barratti* (8); *Esox a. americanus* (8); *Gambusia affinis holbrooki* (7); *Chaenobryttus gulosus* (7); *Enneacanthus gloriosus* (6); *Notemigonus crysoleucas* (6); and *Lepomis macrochirus* (6). All the associated species can tolerate the sluggish, acid, brown-stained waters characteristic of the Atlantic Coastal Plain.

Habits—Specimens kept in aquaria have acted much like *E. fusiforme* (*q.v.*). They rested upon the bottom most of the time and darted forward after food such as white worms, tubificid worms, or pieces of earthworms. Occasionally they swam up into the plants and rested there. As with *E. fusiforme,* there was never any indication of any territoriality.

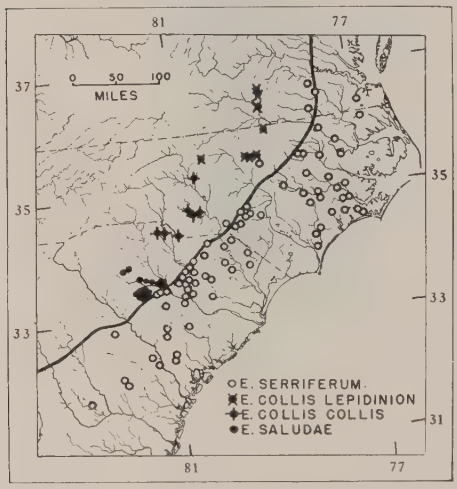


Figure 3. The distribution of *Etheostoma serriferum, E. collis,* and *E. saludae* in relation to the Fall Line. (Based upon specimens examined.

Distribution—Found along the Atlantic Coastal Plain, usually below the Fall Line, from the Dismal Swamp of southeastern Virginia to the Altamaha River of Georgia. This extends the range given by Hubbs and Cannon (1935) south by three river systems. It has been taken above the Fall Line in Mud Creek, a tributary of the Cape Fear River, at Durham, N. C. However, Mud Creek is like a typical sluggish Coastal Plain stream. Another typical Coastal Plain species, *Aphredoderus sayanus,* was also taken here. Figure 3 shows the distribution of *E. serriferum* collections examined.

This distribution coincides with that of *Chologaster cornutus.* Woods and Inger (1957:249-250) commented that there appeared to be no reason why *Chologaster* should not range into the Okefenokee Swamp or west into Alabama. Several species with similar habitat requirements, such as *Gambusia affinis, Aphredoderus sayanus,* and *Elassoma* do range westward on the Gulf side of the former Mississippi Embayment to beyond the Mississippi River. (They also erroneously listed *Umbra pygmaea* in this category. Briggs (1958) and Miller (1958:196) gave the southern distribution as northeastern Florida.) Woods and Inger (1957) concluded that *Chologaster* did once extend west as far as the Mississippi and that during some period of drought during late or even post-glacial times the habitat dried up. The other species named have apparently been able to make their way back into this area but *Chologaster* has not done so. Whether this situation is true for *E. serriferum* is even more problematical than for *Chologaster.*

Geographic Variation—Tables 3-9 give the frequency distribution of the characters examined by river systems. Characters which showed no appreciable variation are presented only in the species comparison tables. These include: number of anal spines (two except for one Neuse specimen with one); supratemporal canal complete (except one Neuse and two Santee specimens); infraorbital canal complete, pelvic elements I, 5 (except for one Santee specimen with I, 6); opercular and preopercular squamation 100-X-T; coronal pore present; pectoral rays 11-13, usually 12; and branchiostegals 5-7, usually 6.

There seem to be two poorly defined groups based on the number of pored lateral line scales (Table 3). Populations in the five northern drainages, Nansemond through Neuse-Ellis Lake, have fewer pored scales ($\bar{x}$:30.00-32.39) than the southern eight populations; Cape Fear through the Altamaha ($\bar{x}$:over 33.75). The total lateral-line scales (Table 4) show a similar trend; the northern group has slightly fewer scales than the southern group.

The mode of dorsal spines is eleven except for the Edisto population, which has a mode of ten (Table 5). Seven populations have modal values of 14 rays in the second dorsal fin (Table 5); the Ellis-Neuse population has a mode of 13, as do also the small samples from the Tar, Combahee, Savanna, Ogeechee, and Altamaha. The modal number of anal rays is seven, except for small samples from the Tar, Savannah, Ogeechee, and Altamaha, where the modes are at six (Table 6).

TABLE 3.

Number of pored lateral-line scales in Etheostoma serriferum

Drainage	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	N	$\bar{x}$
Nansemond									1	1	–	1	1														4	30.00
Chowan							1	1	2	1	2	4	1	1	3	3	–	2	1	1							23	32.39
Roanoke								1	1	–	3	1	4	2	1	2	2	1									18	32.39
Tar				1	–	–	–	1	–	–	1	–	–	1	1	2											7	31.00
Neuse-Ellis L.	1	–	1	–	1	1	1	–	2	5	8	8	1	6	6	6	5	5	1								58	31.95
Cape Fear									1	1	2	2	2	7	5	8	3	2	1	–	2	–	–	1			37	34.24
Pee Dee			1	–	–	–	–	1	3	6	5	7	6	10	14	11	11	7	10	2	6	1	1	–	–	1	103	34.35
Santee						1	1	1	4	5	3	5	3	6	7	6	6	6	10	2	4	2	1	1	–	1	75	34.53
Edisto													1	–	2	–	1	3	1								8	35.63
Combahee											1	–	–	–	–	2	3										6	34.67
Savannah										1	–	–	1	–	1	–	–	–	–	–	1						4	33.75
Ogeechee													1	1	1	–	1										4	33.75
Altamaha																	1										1	

TABLE 4.

Number of total lateral-line scales in Etheostoma serriferum

Drainage	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	N	$\bar{x}$
Nansemond					1	–	–	1	1	–	1													4	51.25
Chowan					1	–	2	6	2	5	2	4	3	–	1									26	52.96
Roanoke					1	–	2	3	3	1	1	2	2	3										18	53.17
Tar						1	3	1	2															7	50.57
Neuse-Ellis L.				2	3	5	8	10	10	9	7	–	3	1	–	1	1							60	51.87
Cape Fear	1	–	–	–	1	2	1	6	3	4	3	8	4	4	3	–	1							41	53.71
Pee Dee				1	1	2	6	3	14	14	13	20	9	7	11	1	2	–	1					105	54.29
Santee							3	1	3	5	10	8	12	6	13	4	8	1	2	2	1	–	1	80	56.59
Edisto							1	–	–	3	–	1	3	–	–	1								9	54.56
Combahee								1	1	–	1	2	–	1										6	54.00
Savannah						1	–	–	–	1	1	–	–	1										4	53.25
Ogeechee							1	–	1	–	2	1												5	53.00
Altamaha														1										1	

TABLE 5.

Number of first dorsal spines and second dorsal rays in Etheostoma serriferum

Drainage	*Dorsal Spines* 9	10	11	12	13	x̄	*Dorsal rays* 11	12	13	14	15	16	17	x̄
Nansemond			3	1		11.25			1	2	1			14.00
Chowan		2	18	6		11.15		1	9	15	1			13.62
Roanoke		2	14	2		11.00			5	12	1			13.78
Tar		2	5			10.71		3	4					12.57
Neuse-Ellis L.	1	9	38	10		10.98	1	10	33	14				13.03
Cape Fear		4	32	6		11.05		2	14	21	4	1		13.71
Pee Dee		7	56	41	1	11.34		6	41	48	10			13.59
Santee	1	13	50	18		11.04			16	46	18	1	1	14.09
Edisto	1	8				9.89			3	4	2			13.89
Combahee			5	1		11.17			4	2				13.33
Savannah			3	1		11.25			3	1				13.25
Ogeechee		1	3	1		11.00			3	2				13.40
Altamaha				1					1					

TABLE 6.

Number of anal rays and of scale rows above and below the lateral line in Etheostoma serriferum

Drainage	*Anal rays* 5	6	7	8	9	x̄	*Above* 3	4	5	10	11	*Below lateral line* 12	13	14	15	x̄
Nansemond		1	1	2		7.25		4		1	2	1				11.00
Chowan	3	9	13	1		6.46	2	24		3	9	10	4			11.58
Roanoke		4	9	5		7.06	1	15	2	1	5	9	3			11.78
Tar		4	3			6.43		4	3	2	—	3	2			11.71
Neuse-Ellis L.	1	22	28	9		6.75	4	38	8	2	22	21	3			11.52
Cape Fear		6	17	17	2	7.36	4	33	4	7	14	14	6	1		11.52
Pee Dee		9	66	29	1	7.21	5	92	8	8	37	44	16			11.65
Santee		12	49	20	1	7.12	1	61	20	1	18	32	28	2	1	12.18
Edisto			6	2	1	7.44		7	2		3	1	5			12.22
Combahee		3	3			6.50		2	4			1	4	1		13.00
Savannah	1	3				5.75		2	2		1	2	1			12.00
Ogeechee	1	3	1			6.00		3	2			1	3			12.75
Altamaha		1						1				1				

The mode of the number of scale rows above the lateral line is four (range three to five) (Table 6); below the lateral line 12 in most populations (range 10-15) (Table 6). The modal number of infraorbital pores is six, of preoperculomandibular pores nine, and of interorbital pores two (Table 7).

The nape, breast and parietal are completely covered with scales with modes of X-T, I-C, and I/PX-C/T, respectively (Table 8). The interorbital squamation in *E. serriferum* shows the greatest geographic variation (Table 9). The northern five drainages (Nansemond, Chowan, Roanoke, Tar, and Ellis-Neuse) have fewer scales in the region ($\bar{x}$:9.50-13.81) than the eight southern drainages ($\bar{x}$:17.00-23.25). This reduced squamation is correlated with the reduced number of pored and total lateral-line scales in the same drainages. This same trend is shown in *E. fusiforme*, except that the geographic break between the subspecies of *E. fusiforme* comes between the Cape Fear and Pee Dee, rather than between the Neuse and Cape Fear. The break between subspecies of *E. collis* also occurs in this region, although I am not yet certain whether it is between the Roanoke and Cape Fear or between the Cape Fear and Pee Dee; the latter seems more likely.

This roughly clinal north-south difference, coupled with the lesser differences in pored and total lateral-line scales, indicates differentiation at the racial level.

Specimens Examined—Complete locality data are listed for the Nansemond drainage (northern limit of range), the Tar drainage (new record), and for the Savannah, Ogeechee, and Altamaha drainages (southern limit of range and new locality records). Other collections are listed by drainage, state,

TABLE 7.
Number of pores in infraorbital (INF), *preoperculomandibular* (POM), *and interorbital* (INT) *canals in Etheostoma serriferum*

	INF					POM				INT		
Drainage	4	5	6	7	8	7	8	9	10	0	1	2
Nansemond			3	1				4				4
Chowan		1	21	4			2	24		1	6	19
Roanoke			15	3				18			1	17
Tar			6					5	2	1	–	6
Neuse-Ellis L.			40	10	1		1	47	2	3	9	37
Cape Fear	1	2	35	4			5	35		1	7	32
Pee Dee		2	87	15	1	2	8	93		15	20	70
Santee		1	63	14	3		8	71	2	12	19	50
Edisto			7	2				9			2	7
Combahee			4	2				6			1	5
Savannah			3	1				4			2	2
Ogeechee			5					5				5
Altamaha			1					1				1

TABLE 8.
Squamation of nape, breast, and parietal regions in Etheostoma serriferum

	Nape				Breast				Parietal			
Drainage	PX-T	PX/X-T	X-T	I-C	I/PX-C/T	PX-C/T	PX/X-T	I-C	I/PX-C/T	PX-T	PX/X-T	X-T
Nansemond	1	–	3	4					4			
Chowan			10	13	2				12	–	3	
Roanoke			12	12	3				8	4	3	
Tar	2	4	–	6					6			
Neuse-Ellis L.		4	12	18	7				19	5	1	
Cape Fear		1	9	13	7	–	1		10	3	6	3
Pee Dee			12	12	8	2		1	11	3	6	1
Santee		1	10	14	6	1		1	8	6	3	3
Edisto			9	4	5				1	–	1	7
Combahee		3	3	4	2					1	2	3
Savannah			3	3					3	1		
Ogeechee			4	4						4		
Altamaha			1		1						1	

TABLE 9.

Number of interorbital scales in Etheostoma serriferum

Drainage	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	$\bar{x}$
Nansemond	1	–	–	–	1	–	–	–	–	–	–	–	–	1																	11.67
Chowan			1	–	2	1	1	2	2	2	2	–	1	–	1																13.67
Roanoke	1	–	3	1	2	–	–	1	1	2	2	1	–	–	–	–	1														12.47
Tar	1	1	1	1	–	–	1	–	–	1																					9.50
Neuse-Ellis L.		1	2	3	3	–	–	4	3	1	2	1	3	–	–	1	1	–	1												13.81
Cape Fear							1	2	1	–	2	1	4	2	–	2	1	3	–	–	1										18.50
Pee Dee										6	1	–	3	1	2	2	2	1	–	1	1										18.95
Santee				1	–	–	1	1	1	1	2	2	2	1	–	–	2	–	1	–	–	1	1	–	1	1	1				20.00
Edisto								2	–	2	–	–	–	1	–	–	1	1	1	–	1										18.89
Combahee								1	–	–	–	2	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	1	22.33
Savannah													1	–	1	–	1	–	–	–	–	–	–	–	–	–	–	1			23.25
Ogeechee									1	1	–	–	–	–	–	–	1														17.00
Altamaha													1																		

ounty, and museum number. Complete data n almost all specimens examined are in Collette (1960). A total of 447 specimens rom 112 collections was examined.

Nansemond Dr., Va.—Nansemond Co.: CU 9920 4, 34-41); trib. of Nansemond R., 2 mi. N of uffolk on US 460; March 29, 1941.

Chowan Dr., 26 specimens. Va.—Dinwiddie Co.: U 11781. Greensville Co.: CU 20623, 29976. ussex Co.: CU 16881. N.C.—Gates Co.: CU 802, 30141.

Roanoke Dr., 18 specimens. N.C.—Bertie Co.: U 29979. Martin Co.: CU 25241, 29981. Northampton Co.: CU 17017.

Tar Dr., N.C.—Edgecomb Co.: USNM 179732 1.26); Fishing Cr., Tarboro; Sept. 19, 1959. ash Co.: DU uncat. (4, 42-46); Little Sapony r., 3.6 mi. W of Nashville on US 64; June 1, 950. DU uncat. (2, 43-46); Little Sapony Cr., 3 mi. S of Nashville on NC 58; June 1, 1950.

Neuse-Ellis Lake Dr., 94 specimens. N.C.—arteret Co.: DU uncat. Craven Co.: USNM 3041; CU 9878, 9814, 16821, 29982, 29984; out f UMMZ 161986; DU uncat. Johnston Co.: SNM 179730. Lenoir Co.: CU 9723, 9748. Onlow Co.: CU 9752, 30573. Pitt Co.: DU uncat. Vayne Co.: CU 33105. Wilson Co.: CU 10636. Vake Co.: UMMZ 107053 (1, 52); Buffalo Cr., Vendell; Nov. 19, 1925; holotype of *Hololepis errifer*.

Cape Fear Dr., 60 specimens. N.C.—Bladen Co.: U 34529. Brunswick Co.: CU 4090. Cumberland o.: CU 14100, 30134. Duplin Co.: CU 30557. urham Co.: DU uncat.; CU 34517. Hoke Co.: U 15614, 25948, 26109, 33102. Moore Co.: CU 5262, 32170; USNM 93193. New Hanover Co.: SNM 93132, 93133, 86163 paratypes of *Hololepis errifer*. USNM 170975, 94348. Pender Co.: CU 9986, 30052, 33103, 33104.

Pee Dee Dr., 134 specimens, N.C.—Moore Co.: U uncat.; CU 11147, 32706, 35134. Richmond o.: CU 19571. Richmond-Scotland cos.: UG 460. cotland Co.: CU 25965. S.C.—Chesterfield Co.: U 15636, 29989, 29990. Clarendon Co.: CU 5202, 15359. Darlington Co.: CU 15721, 28206, 0122. Dillon Co.: CU 15867. Florence Co.: CU 9188. Lee Co.: CU 28220. Marion Co.: CU 25225. Marlboro Co.: ANSP 61027-9. Sumter-Lee cos.: U 15225.

Santee Dr., 80 specimens, S.C.—Calhoun Co.: U 35051. Kershaw Co.: CU 35042, 35061, 35056, 5059, 35060, 35064, 35055, 35047. Lexington o.: CU 35058, 35050, 35063. Richland Co.: U 35049, 35054, 35046, 35057, 35043, 35053. 5044, 35062, 35052, 35048, 35045.

Edisto Dr., 9 specimens, S.C.—Aiken-Lexington os.: CU 35041. Bamburg Co.: CU 35065, 35066.

Combahee Dr., 6 specimens, S.C.—Allendale Co.: U 15322. Bamburg Co.: CU 19194. Hampton o.: CU 32672. Jasper Co.: CU 32661.

Savannah Dr., Ga.—Richmond Co.: CU 30321 1.39); Boggy Gut Cr., trib. of Brier Cr., 22.5 ni. SW of Augusta on US 1; March 24, 1950. Screven Co.: CU 30621 (2, 45); trib. of Savannah R., 12.9 mi. SW of Savannah R., Dec. 8, 1949. UG 240A (1, 50); Blue Sp., Black r., 6 mi. NE of Newington; Jan. 31, 1952.

Ogeechee Dr., Ga.—Candler Co.: UG 152 (2, 40-44); March 24-25, 1950 and UG 152A (1, 30); March 24-25, 1950 and out of UG 152B (1, 29); Aug. 8, 1958; Canoochee R., 4 mi. W of Metter on Ga 46. Emmanuel Co.: UG 554 (1, 44); Canoochee R., 8 mi. S of Twin City; Aug. 8, 1958.

Altamaha Dr., Ga.—Telfair Co.: CU 17257 1, 45); Little Ocmulgee R., 1.2 mi. N of McRae on US 319; March 25, 1950.

Etheostoma gracile (Girard)

Boleosoma gracile—Girard, 1859:103 (original description).

Poecilichthys butlerianus—Hay, 1882:61-62 (original description).

Poecilichthys palustris—Gilbert, 1884: 209-210 (original description).

Boleichthys fusiformis—Forbes, 1907: 281; 287, 291-292, map XV (in part) (ecology, Ill.); Forbes, 1909:390, 401, 403, 417, 421, 425, 432, tables I-VI, map XCVIII, pl. XXV (in part) (ecology and distribution, Ill.); Forbes and Richardson, 1909, 1920:315, map 98 (in part) (description and distribution, Ill.); Forbes, 1914:17, map 48 (in part), fig. 30 (distribution in Ill., not given by Hubbs and Cannon, 1935, in their synonymy); Thompson and Hunt, 1930:33, 45 (ecology, Champaign Co., Ill.); Driver, 1942:285 (in key, in part).

Hololepis fusiformis—Luce, 1933:120 (Ill.); O'Donnell, 1935:489-490 (in part) (Ill.).

Hololepis gracilis—Hubbs and Cannon, 1935; Baker, 1939a:36-37 and 1939b:45 (Reelfoot Lake, Tenn.); Kuhne, 1939:93, fig. 63; Lamb, 1941:45 (San Jacinto R., Tex.); Fowler, 1945:40 (Ala., Pearl, Trinity, Nueces r.), 369-370 (La.); Gerking, 1945:16, 95 (distribution in Ind.); Hubbs, 1946:39 (Okla.); Moore and Poole, 1948: 37 (McCurtain Co., Okla.); Baughman, 1950:247 (Tex.); Hall, 1951:17 (Lake Murray, Carter and Love cos., Okla.); Cross and Moore, 1952:409 (Poteau River in Okla. and Ark.).

Boleichthys gracilis—Blatchley, 1938:98-99 (Ind.); Driver, 1950:298 (in key).

Boleichthys fusiformis gracilis—Schrenkeisen, 1938:235.

Etheostoma gracile—Hubbs, 1952:486 (Tex.); Moore, 1952:11 (Okla.); Jurgens and Hubbs, 1953:4 (Tex.); Knapp, 1953: 126, 128 (Tex.), fig. 166; Cross, 1954:478-479 (Kan.); Bailey and Gosline, 1955:20, 44 (number of vertebrae); Gerking, 1955: 84 (Ind.); Gunning and Lewis, 1955:557 (Ill.); Linder, 1955a:28-29 (in aquaria); Linder, 1955b:176 (Blue R., Okla.); Eddy, 1957:219, fig. 545; Hubbs, 1957a:9 (Tex.); Hubbs, 1957b:93, 98 (distribution in Tex.); Moore, 1957:197-198; Bridges, 1958:3, 9 (poisoned in Ill. farm ponds); Hancock and Sublette, 1958:49 (La.); Hubbs, 1958: 11 (Tex.); Blair, 1959 (Okla., distribution, ecology); Boudreaux, Strawn, and Callas, 1959:8, 10 (poisoned in Tex.); Cook, 1959: 35, 38, 200, 207-208 (Miss.); Hubbs, 1959: 50, 52 (artificial hybridization with *Percina sciera* and *Etheostoma proeliare*); Riggs and Bonn, 1959:167 (Lake Texoma, Okla.); Collette, 1961:2051.

Types—Hubbs and Cannon (1935) selected USNM 1328, 36 mm SL, as lectotype of *Boleosoma gracile;* from Rio Seco, near Fort Inge, Texas, collected by Dr. Kennerly. They listed two extant paratypes: MCZ 113, from the lectotype locality, and USNM 1329, from Leona River, near Fort Inge, Texas, also collected by Dr. Kennerly. The holotype of *Poecilichthys butlerianus* is USNM 32224, 43 mm SL, from a pool along the Big Black River, near Vaughan's Station, Yazoo Co., Mississippi. Hubbs and Cannon selected USNM 34983, 30 mm SL, from Switz City Swamp, Indiana, as lectotype of *Poecilichthys palustris.*

Diagnosis—Similar to *E. zoniferum* in usually having: ten preoperculomandibular pores; interorbital pores absent; naked breast and nape; and green vertical bars on the sides in life. Differs from *E. zoniferum* primarily in having the infraorbital canal complete with eight pores. Also differs in having more anal rays ($\bar{x}$:6.7), more scales above the lateral line (mode:4, $\bar{x}$:3.7) and below the lateral line (mode:9, $\bar{x}$:8.9). Maximum size of males 43.4 mm SL and females 46.4 mm (TNHC 578, Neches River, Tex.).

Coloration—In the non-breeding female, groups of medium sized melanophores are present on the membrane at the base of the first dorsal fin and small melanophores are found on the distal margin of the membranes between the last three dorsal spines. Medium melanophores are scattered on the membranes of the second dorsal fin and do not form the rectangular blotches present in *E. saludae* and *E. collis.* The pectoral fin is clear, but a few small melanophores outline the rays. The pelvic fin varies from clear to having a few melanophores on the last rays and on the membranes between them. The caudal is barred. The belly and breast are immaculate, or have a few scattered melanophores. There are a few scattered medium melanophores on the cheek. The preorbital and postorbital bars are prominent; the supraorbital and suborbital are faint. The pored portion of the lateral line usually is light, although some specimens have a few melanophores under the scales and/or along their distal edge. The median basi-caudal spot is usually prominent. Sometimes there are faint spots at the upper and lower bases of the caudal fin. The pattern of the sides varies within, as much as between, populations. Some specimens have no lateral blotches while others show, more or less clearly, eight to ten which alternate with the dorsal saddles and give the fish a variegated pattern. The eight to eleven dorsal saddles connect at the level of the lateral line and isolate central light areas. There is no pigment on the genital papilla or in an area around it. Figure 4 compares a breeding female *E. gracile* with *E. zoniferum.*

The pectoral and caudal fins, dorsal body surface, and genital papilla in the non-breeding male are colored like the female. The dorsal fins are darker than those of the female. The anal fin is covered with large melanophores which tend to fuse. The pelvic fins have many melanophores between the last two rays and fewer between the anterior rays. The breast and belly usually are covered with small melanophores. The orbital bars and lateral blotches appear less prominent in the non-breeding male because the cheek and sides are darker than in the female. The pored portion of the lateral line has more pigment on the distal than on the proximal parts of some scales. The non-pigmented area around the genital papilla is smaller than in the females and appears more prominent, because of the darker venter.

In the breeding male, the pectoral and caudal fins, pored portion of the lateral line, orbital bars, basi-caudal spots, sides, dorsal surface, and genital papilla are colored like the non-breeding male; the other regions are darker. Most of the basal third of the first dorsal fin is solid black. The second dorsal and anal fins show a lesser tendency toward melanophore fusion. The pelvic fins, breast and belly are densely speckled with small melanophores. The cheek is usually darker. Figure 4 compares the pattern of breeding male *E. gracile* and *E. zoniferum.*

In life, *E. gracile* and *E. zoniferum* differ from the other species of the subgenus *Hololepis* in having vertical green bars on the sides. Males of both species have a submarginal red-orange band in the first dorsal fin which intensifies at breeding season. Hubbs and Cannon (1935) quoted Jordan and Evermann (1896) to the effect that the spinous dorsal in life is usually bright blue. This is an obvious reference to the

olor of a breeding male *Etheostoma exile* hich Jordan confounded with *E. gracile*.

Breeding Tubercles—At the height of the reeding season, moderately large tubercles re present on the distal half of the anal rays (Fig. 1h), the distal three-quarters of the lower side of the pelvic spine and rays (Fig. 1k), and in two rows of four tubercles on each ramus of the lower jaw (Fig. 1m). The earliest that tubercles were ob-

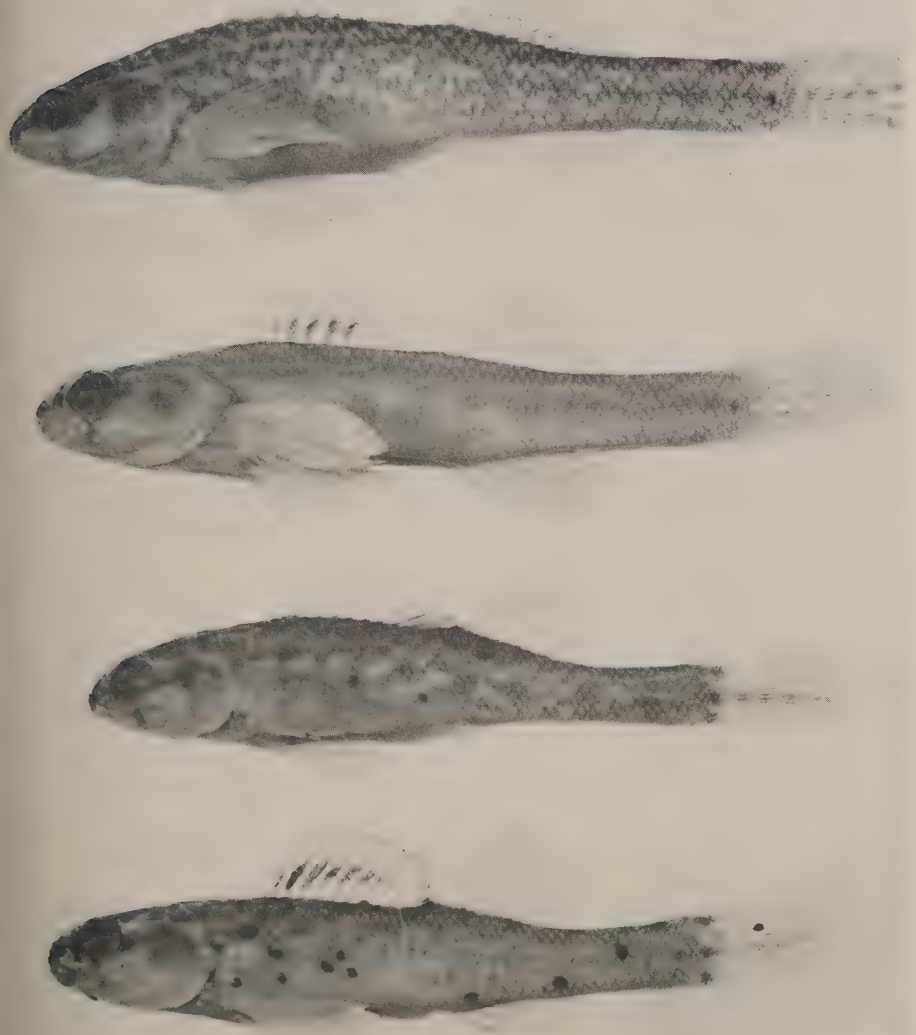


Figure 4. Breeding patterns of *Etheostoma gracile* and *E. zoniferum*. (from top to bottom) *E. gracile* female; UMMZ 161034; 42.7 mm; Tenn., Haywood Co., Ohio-Arkansas dr.; Apr. 2, 1949. *E. gracile* male; TNHC 2957; 38.7 mm; Tex., Montgomery Co., San Jacinto dr.; Mar. 7, 1952. *E. zoniferum* female; UMMZ 163758; 35.3 mm; Ala., Greene Co., Tombigbee dr.; Apr. 16, 1941. *E. zoniferum* male; UMMZ 163758; 36.5 mm; Ala., Greene Co., Tombigbee dr.; Apr. 16, 1941. (Photographs by Douglass M. Payne)

TABLE 10.

Number of pored lateral-line scales in Etheostoma zoniferum and E. gracile

Species and drainage	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	$\bar{x}$
zoniferum																						
Alabama	1	–	–	1	–	1	2	3	6	2	2	3	2	1								15.21
Tombigbee											2	–	1	1								18.25
gracile																						
Tombigbee										1	–	1	–	–	–	2	3	–	–	–	1	21.75
Pearl														2								20.00
Mississippi																						
Wabash								1	–	3	–	4	7	7	4	5	1	–	1	1		19.85
Ohio								1	–	2	3	5	6	12	5	2	2	3	2			19.95
Wabash-Miss.									1	1	–	3	7	3	9	5	2	2	–	1		20.50
to Missouri										1	4	3	4	2	–	1						18.40
Missouri-Ohio										1	3	2	9	8	6	2	5	3	4	5	1	21.39
Ohio-Arkansas								1	1	1	6	4	3	3	7	2	1	2	1	1	1	19.88
Yazoo-Big Black											3	2	3	–	2	1	–	1				19.33
Red-Ouachita							1	5	10	14	17	29	38	27	23	15	14	5	1	1		19.18
Arkansas									2	–	9	7	8	12	15	8	9	1	1			20.11
Lower Miss.									1	–	–	1	–	1	–	1						18.75
Total Miss.							1	8	15	23	45	60	85	75	71	42	34	17	10	9	2	19.76
West of Miss.																						
Vermilion										1	3	–	1	–	1							17.83
Calcasieu											1	–	2	2	1							19.33
Sabine								2	3	6	4	4	1	2	2							17.08
Neches								7	5	8	6	14	11	10	8	4	–	2	–	2		18.44
Trinity								1	1	2	4	6	6	8	9	1	–	–	1	1		19.33
San Jacinto							1	1	–	1	6	9	12	10	10	3	2	1	2	1		19.61
Brazos								1	–	2	3	5	4	4	1	1	–	1				18.64
Colorado										2	5	1	12	4	13	6	5	2				20.22
Navidad													1									
Guadalupe										2	–	–	3	3	3	1	1					19.77
Nueces										1	1	1	3	2	2	1	–	–	–	1		19.83

erved was February 19 (TNHC 4994; 1, 9.4 mm; Red River, Tex.). The latest that reeding tubercles were found was April 9 (UK 2418; 3, 33.6-39.6 mm; Red River, Okla.). The maximum development appears o take place in mid-March in Texas, where ollections taken from throughout the year ave been examined.

Genital Papilla—The genital papilla of he breeding female is a moderately elongate ube with a somewhat blunt end. A 36.7 mm female (UMMZ 162897) taken from he Yazoo River of Mississippi has a genital papilla which is 1.7 x 0.7 mm. Figure 1c hows the genital papilla of a 40.4 mm fe- nale taken on Mar. 7 (TNHC 2750, San acinto R.). There is a bulbous enlargement f the base of the papilla in some specimens.

Development—As in *Etheostoma fusi- orme,* the supratemporal canal is incom- lete in juveniles and the two ends of the anal fuse with age. A series of 25 Mis- issippi specimens (USNM 129113), rang- ng from 12.5 to 20.7 mm, all have incom- plete supratemporal canals. Again, as in *E. fusiforme,* the transition period from in- complete to complete takes place at differ- ent sizes in different populations. This is shown by two groups of collections (UMMZ 107048, Missouri to Ohio Drainage; USNM 172570, 172495, 172523, 172481, 172576, and 172560 from the Red River Drainage). Of the thirty specimens in UMMZ 107048, five (19.4-21.0 mm) have incomplete supra- temporal canals, while the other 25 (26.7- 34.7 mm) have complete canals. Eight of the Red River specimens (14.6, 14.7, 16.1, 16.5, 16.5, 17.1, 17.4, 23.4 mm) have in- complete canals while the larger specimens (17.7, 17.7, 18.7, 19.1, 25.5, 27.5, 34.1, 35.4 mm) have complete canals.

Development of the pored lateral-line scales is also very similar to that in *E. fusi- forme* (*q.v.*) as shown in USNM 129113. Eleven specimens (18.1-20.7 mm) have from 10 to 16 pored lateral-line scales which is below the normal range of 13-27, mean 19.5 (Table 39). Six specimens (17.4-

TABLE 11.
Number of total lateral-line scales in Etheostoma zoniferum and E. gracile

Species and drainage	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	$\bar{x}$
oniferum																	
Alabama		2	1	–	–	2	1	6	6	3	1	–	1	1			47.17
Tombigbee									1	2	–	1					49.25
racile																	
Tombigbee										1	1	2	1	1			51.00
Pascagoula										1							
Pearl								1	1								47.50
Mississippi																	
Wabash					1	4	5	7	4	5	6	3	2				48.03
Ohio			1	–	3	3	6	7	7	7	4	3	1	–	2		47.86
Wabash-Miss.			1	1	2	4	6	8	4	5	2	2					46.97
to Missouri					1	1	1	3	1	1	2	3	–	1			48.50
Missouri-Ohio				1	3	2	5	4	7	6	4	10	1	5	1		48.86
Ohio-Arkansas			2	2	3	1	3	4	3	6	3	4	1				47.41
Yazoo-Big Black		1	–	–	2	3	2	3	1	–	–	1					45.85
Red-Ouachita	1	3	5	7	7	21	24	40	35	18	19	11	6	3	–	1	47.31
Arkansas					2	5	4	6	15	12	6	9	4	2			48.62
Lower Miss.		1	–	–	–	–	1	2									45.25
Total Miss.	1	5	9	11	24	44	57	84	77	60	46	46	15	11	3	1	47.70
West of Miss.																	
Vermilion						1	3	–	1	1							46.67
Calcasieu			1	1	–	1	2	–	–	–	1						45.33
Sabine		2	1	1	–	3	5	5	2	1	1	1	–	1			46.35
Neches	1	4	6	9	3	11	8	12	16	5	3	1					45.77
Trinity		1	2	2	1	8	4	6	11	3	–	1	1	1			46.63
San Jacinto	1	–	2	3	5	6	8	10	10	6	1	3	4	1	–	1	47.11
Brazos						2	3	3	2	3	2	3	2				48.45
Colorado						3	–	1	3	6	12	9	8	7	1		50.40
Navidad								1									
Guadalupe					1	–	1	–	5	1	2	–	1				48.27
Nueces									2	1	1	3	3	2			50.83

TABLE 12.

Number of first dorsal spines and second dorsal rays in Etheostoma zoniferum and E. gracile

Species and Drainage	First Dorsal								Second Dorsal							Abnormal
	7	8	9	10	11	12	13	$\bar{x}$	9	10	11	12	13	14	$\bar{x}$	
zoniferum																
Alabama		3	10	7	4			9.50	1	7	13	3	1		10.84	–
Tombigbee			1	1	2			10.25		3	1				10.25	–
gracile																
Tombigbee			6	2				9.25		1	4	2	1		11.38	–
Pascagoula			1							1						–
Pearl			1	–	1			10.00		1	–	1			11.00	–
Mississippi																
Wabash		3	23	11				9.22		5	22	9	1		11.16	–
Ohio		2	26	13	1			9.31			23	17	2		11.50	I, 11; I, 12
Wabash-Miss.		2	17	13	2			9.44		5	21	8			11.09	I, 11
to Missouri		1	5	11				9.59			15	2			11.12	–
Missouri-Ohio		4	34	20				9.28		5	21	29	3		11.52	I, 11
Ohio-Arkansas	1	1	16	13	2			9.42		1	19	12	1		11.39	I, 11
Yazoo-Big Black		1	8	4				9.23		3	6	4			11.08	–
Red-Ouachita		9	121	68	3	1		9.34	1	26	107	58	10		11.25	I, 10; I, 11; I, 11
Arkansas	1	13	48	9				8.92	1	26	38	6			10.69	I, 9; I, 10
Lower Miss.		1	2	1				9.00		2	–	2			11.00	–
Total Miss.	2	37	300	163	8	1		9.28	2	73	272	147	17		11.20	–
West of Miss.																
Vermilion		2	5					8.71		1	3	3			11.29	–
Calcasieu			5	1				9.17		2	3	1			10.83	–
Sabine			12	6	1			9.42		2	15	2			11.00	I, 10
Neches		10	48	17	–	–	1	9.14		7	47	21	1		11.21	–
Trinity		4	25	10				9.15		6	16	14	3		11.36	–
San Jacinto	1	7	35	21	1	–	1	9.27		5	47	13	1		11.15	I, 11
Brazos		3	14	6				9.13		1	11	10	1		11.48	–
Colorado		3	40	9				9.12		1	22	27	1	1	11.60	–
Navidad			1								1					–
Guadalupe		3	8	1				8.83		3	7	2			10.92	I, 10
Nueces			6	4				9.40		2	7	1			10.90	–

(The abnormal specimens with a spine in the anterior part of the second dorsal fin are not included in the frequency distributions or means.)

TABLE 13.
Number of anal rays in Etheostoma zoniferum and E. gracile

ecies and Drainage	4	5	6	7	8	9	$\bar{x}$
niferum							
Alabama	1	6	11	7			5.96
Tombigbee		2	2				5.50
acile							
Tombigbee			3	4	–	1	6.88
Pascagoula		1					
Pearl			2				6.00
ississippi							
Wabash			8	24	2		6.82
Ohio			6	32	6		7.00
Wabash-Miss.			18	17	1		6.44
to Missouri			7	10			6.59
Missouri-Ohio			10	34	3		6.85
Ohio-Arkansas			6	26	2		6.88
Yazoo-Big Black			6	5	2		6.69
Red-Ouachita		1	93	99	12		6.60
Arkansas		1	35	36	1		6.51
Lower Miss.			2	1	1		6.75
Total Miss.		2	191	284	30		6.67
est of Mississippi							
Vermilion			4	3			6.43
Calcasieu			5	1			6.17
Sabine			10	10			6.50
Neches		2	44	37	2		6.46
Trinity			16	22	1		6.62
San Jacinto		1	24	40	1		6.62
Brazos			8	15			6.65
Colorado			2	34	16		7.27
Navidad				1			
Guadalupe			3	10			6.77
Nueces			1	7	1		7.00

.0 mm) have 0-13 pored scales. Five ecimens (15.9-17.1 mm) have either one no pored scales, while the three smallest ecimens (12.5-14.9 mm) have no pored ales. From 18.0 mm down, all the speci-ens in this collection have ridges on some the scales in the lateral line posterior to e completely pored scales. These ridges ow out from the scale and then meet over e center of the scale forming the pored teral-line scale.

The development of squamation was also udied in this collection. The smallest 2.5 mm) specimen has scales on the sides the caudal peduncle and extending for-ard along the lateral line. Scales are absent the ventral part of the caudal peduncle, pe, pectoral fin base, opercle, preopercle, lly, and dorsally and ventrally from the teral line anterior to the first dorsal fin gin. At 14.6 mm, a few imbedded scales pear on the opercle and squamation of e ventral half of the belly begins. Between 0 and 20.7 mm, squamation of the oper-cle, preopercle, and the posterior part of the belly is complete. Scales develop on the nape and the base of the pectoral fin some time after this.

The most interesting developmental feature that can be studied in this collection is the infraorbital canal. In adult *E. gracile,* it is complete with eight pores. In all 25 specimens in USNM 129113, this canal is incomplete. The 12.5 mm specimen has two pores in the anterior portion of the canal and only an open groove in the posterior portion of the canal. Most of the middle nineteeen specimens (14.6-19.0 mm) have three pores in the anterior portion and two in the posterior ($2+3$ as in *E. fusiforme*) but there are also two specimens with $3+3$ and two with $2+4$. The largest five specimens in the collection have $3+4$. In addition, the 20.7 mm specimen has a groove extending between the anterior and posterior portions of the canal. This groove has lateral ridges along it which will roof over the canal in a manner similar to the development of the

TABLE 14.

Number of scale rows above and below the lateral line in Etheostoma zoniferum and E. gracile

Species and Drainage	Above						Below					
	2	3	4	5	6	x̄	7	8	9	10	11	12
zoniferum												
Alabama		20	5			3.20	5	11	7	2		
Tombigbee		2	2			3.50	1	1	2			
gracile												
Tombigbee		8				3.00		3	4			
Pascagoula		1						1				
Pearl		1	1			3.50		1	1			
Mississippi												
Wabash		14	21	1		3.64		10	19	6	2	
Ohio		19	14	1		3.47		9	16	9		
Wabash-Miss.	1	23	8			3.22	1	11	17	5		
to Missouri		2	14			3.88		7	9			
Missouri-Ohio		22	29	4		3.67	4	25	17	7	1	
Ohio-Arkansas		20	13			3.39	1	10	13	8		
Yazoo-Big Black		7	5	1		3.54		4	7	1	1	
Red-Ouachita	1	71	121	13		3.71	10	56	80	45	10	1
Arkansas		28	33	2		3.59		20	30	14	4	
lower Miss.		3	1			3.25		2	—	1	1	
total Miss.	2	209	259	22		3.61	16	154	208	96	19	1
West of Miss.												
Vermilion		1	2			3.67		1	2			
Calcasieu	1	4				2.80	1	2	2			
Sabine		5	15			3.75		3	13	4		
Neches		24	51	6		3.78	1	26	39	12	1	1
Trinity		3	29	9		4.15		5	15	15	4	
San Jacinto		16	39	10		3.91		13	26	18	2	
Brazos		10	11			3.52		10	9	3		
Colorado		6	32	13	1	4.17	1	15	28	8		
Navidad			1					1				
Guadalupe			10	1		4.09		3	6	—	2	
Nueces		1	5	5		4.36		1	4	4	1	1

pored lateral-line scales. It will be noted that development in the infraorbital canal proceeds from the pore just behind the nostril posteriorly *and* from the junction with the lateral canal anteriorly.

Habitat—Data on 50 University of Texas collections made available by Clark Hubbs show that most *E. gracile* were found in slow, moderately flowing, or quiet waters (Table 17). The type of water was about equally divided between muddy and/or murky, clear, and brown. No aquatic vegetation was present at about half the collection localities and most of the rest had only slight to moderate amounts (*Myriophyllum, Potamogeton, Typha,* green algae, and water lilies). Aquatic vegetation was abundant at only four localities and was composed of *Ceratophyllum,* rushes, and filamentous algae. The number of times each of the six elements in the bottom types—mud and/or slit, sand, detritus, gravel, clay, and bedrock —were present is given in Table 17. The most often found bottom type was r and/or silt (present at 77% of the lo ities).

All *E. gracile* in 12 collections I made Illinois, Indiana, Tennessee, Oklahoma, Texas, were taken from ponds, swamps backwaters. Eight localities lacked aqu vegetation. One had slight amounts of gae, another some emergents, and a thi few aquatics. The north end of Reel Lake, Tennessee, had abundant aquatic v tation, including *Cabomba, Azolla, Cer phyllum,* and *Ludwigia.* The water white and turbid at 11 localities; turbid slightly stained brown in the other. At localities, *E. gracile* was taken over n silt or detritus.

Blatchley (1938) reported the hab of *E. gracile* in Indiana as lowland swa and bayous; Gerking (1945) as slugg turbid water on a rather firm bottom sand (or sand and mud). In Illinois, O'D nel (1935) reported that *E. gracile*

TABLE 15.

Number of pores in preoperculomandibular and infraorbital canals in Etheostoma zoniferum and E. gracile

Species and Drainage	Preoperculomandibular						Infraorbital										
	8	9	10	11	12	$\bar{x}$	2+3	2+4	3+4	3+5	2+6	6	7	8	9	10	$\bar{x}$
zoniferum																	
Alabama		2	19			9.90	2	17	4								2+4
Tombigbee			4			10.00		4									2+4
gracile																	
Tombigbee			6	–	1	10.29							1	5			7.83
Pascagoula			1											1			
Pearl			2			10.00								2			8.00
Mississippi																	
Wabash		1	33			9.97							12	22			7.65
Ohio		1	43			9.98							16	26			7.62
Wabash-Miss.		1	27	1		10.00							5	30			7.86
to Missouri	1	1	12	3		10.00								13	3		8.19
Missouri-Ohio		1	46	1		10.00					1*	1	12	32			7.69
Ohio-Arkansas		3	29	1		9.94						1	5	23	3		7.88
Yazoo-Big Black			13			10.00							1	12			7.92
Red-Ouachita	1	13	186	3		9.94				1*			16	160	22	1	8.04
Arkansas	2	18	51			9.69							6	56	7		8.01
lower Miss.			3	1		10.25								4			8.00
total Miss.	4	39	443	10		9.93						2	73	378	35	1	7.92
West of Miss.																	
Vermilion		1	6			9.86								4	3		8.43
Calcasieu		1	5			9.83							1	5			7.83
Sabine			19	1		10.05							3	14	3		8.00
Neches	1	5	66	1		9.92							9	64	2		7.91
Trinity		4	33	2		9.95							2	37			7.95
San Jacinto		5	57	4		9.98							5	55	4	3	8.07
Brazos		4	19			9.83							1	21			7.95
Colorado		4	45	2		9.96							5	43	4		7.98
Navidad			1											1			
Guadalupe			8	2		10.20							1	10	1		8.00
Nueces		1	7			9.88								9	1		8.10

* Abnormal. Not included in calculation of means.

TABLE 16.

Squamation of preopercle, opercle, and nape in Etheostoma zoniferum and E. gracile

Species and Drainage	Preopercle (100% scaled)				Opercle (100% scaled)				Percent of Nape Scaled												
	I/PX-C/T	PX-T	PX/X-T	X-T	I/PX-C/T	PX-T	PX/X-T	X-T	0	10	20	30	40	50	60	70	80	90	100	Nape x̄%
zoniferum																				
Alabama	4	1	4					10	9	1										1
Tombigbee		3	1					4	3	1										3
gracile																				
Pascagoula				1				1			1									20
Pearl				1				1												–
Mississippi																				
Wabash	2	2	2	5	5	2	4		1	1	1	1	–	–	–	–	1	1	5	66
Ohio				9				9			1	1	–	–	–	–	1	1	5	80
Wabash-Miss.				13	3	3	4	3	1	1	1	3	–	–	–	–	–	1	4	65
to Missouri				3				3						1	–	–	–	1	1	80
Missouri-Ohio			1	4		1	4			2	1	–	–	1	1					30
Ohio-Arkansas				14			6	8		1	–	–	–	2	2	1	–	3	5	76
Red-Ouachita		1	4	9	1	3	1	9	2	1	2	–	1	–	–	–	–	2	5	59
Arkansas		1	2	6	1	–	6	1	4	–	1	–	1	–	–	–	–	2	1	38
lower Miss.			1	1			1	1									2			80
total Miss.	2	4	10	64	10	9	26	34	8	6	7	5	2	4	3	1	4	11	26	62
West of Miss.																				
Calcasieu				4		2	1	1	2	1	–	1								10
Sabine	2	2	4	1		5	5	1		3	1	1	1	–	–	–	2	2	1	51
Neches			5	6		3	6	2		1	–	–	–	–	–	–	1	3	6	87
Trinity				8		2	5	1		1	–	–	–	–	–	–	1	–	6	86
San Jacinto			1	6		2	3	2			1	–	–	–	–	1	–	–	5	84
Brazos				10				10											8	100
Colorado			1	11	1	5	4	1											12	100
Navidad				1				1			1									
Guadalupe			4	5			4	5				2	–	–	–	1	1	–	7	76
Nueces			1	8			1	8		1	–	–	–	–	–	–	2	2	4	83

TABLE 17.
Habitat data for Etheostoma gracile collections from Texas

ater Current	Number of collections	Percent of collections
ne	8	19.0
w	8	19.0
ne to moderate	6	14.3
w to moderate	5	11.8
derate	4	9.5
ne to fast	2	4.8
w to fast	4	9.5
derate to fast	2	4.8
t	3	7.1
al	42	99.8

ater Current	Present in collections	Present in percent of collections
ne	16	38.1
w	25	59.4
derate	23	54.7
t	11	26.2

uatic Vegetation	Number of collections	Percent of collections
ne	22	46.8
ght to moderate	21	44.6
undant	4	8.5
al	47	99.9

ttom Type	Present in collections	Present in percent of collections
d and/or silt	33	76.7
d	22	51.1
tritus	14	32.6
avel	10	23.0
y	7	16.3
drock	5	11.6

red sluggish water and a mud bottom
d Bridges (1958) recorded it from two
m ponds. The information presented by
rbes (1907, 1909, 1914) and Forbes and
chardson (1909, 1920) is not reliable
ce they confounded *Etheostoma exile,* a
cies of cooler, cleaner waters, with *E.*
cile. However, both species prefer water
th little or no flow. Forbes and Richard-
n (1920) found 78% of *gracile-exile* col-
tions in areas of sluggish flow and Forbes
907:303) and Forbes and Richardson
920) reported that 66% of *gracile-exile*
lections were made over muddy bottom.
rbes and Richardson, apparently mistak-
y, reported this in their ecological table
67% over rock and sand. Hancock and
blette (1958) reported it from a sluggish
wn-water bayou in Louisiana. Blair
959) noted that *E. gracile* and *E. chloro-*
num are fishes of sluggish , muddy,
eams and lakes in northeastern Oklahoma.

Species Associates—Forbes (1907) found a large coefficient of association between *Etheostoma chlorosomum* and *E. gracile-exile* in Illinois. However, his figures are not accurate, because he confounded *E. gracile* with *exile*. If the northern collections of the allopatric *exile* could be eliminated the coefficient would be still higher. *Etheostoma chlorosomum* was taken in 6 out of 41 localities in the Poteau River of Oklahoma and Arkansas (Cross and Moore, 1952). At five of these localities, *E. gracile* was also taken. This association was also noted in several of my southern Illinois and Indiana collections. Fishes that are associated with *E. gracile* prefer or tolerate low gradient and/or silty bottoms and turbid water.

Habits—Forbes (1878) and Forbes and Richardson (1920) reported the food of a few Illinois specimens to consist of "larvae

of gnats and of may-flies, with a few copepoda."

Forbes and Richardson reported that females taken in Illinois on April 28 contained "full-sized eggs." Hubbs and Cannon (1935) reported the breeding season in Illinois to be late March and April. Moore and Poole (1948) noted that specimens in an Oklahoma collection of *E. gracile* were "in breeding color" on April 19. Breeding tubercles are present in Texas specimens of *E. gracile* from February 19 to April 19 with their greatest development in mid-March. Therefore, the spawning season in Texas appears to be about mid-March.

The breeding behavior of *E. gracile* and *zoniferum* may differ slightly from that of *E. fusiforme* because these two species possess accessory breeding tubercles on the lower jaw rami. Perhaps the male rubs his chin along the nape of the female during courtship. The red in the first dorsal fin of male *E. gracile* and *zoniferum* indicates the presence of territoriality. My aquarium observations of *E. gracile* have indicated this with a dominant male occupying the corner of an aquarium where they were fed. This dominance was indicated by brighter colors and by chasing intruders. Also, pairs of male *gracile* have been observed spreading their dorsal fins at each other in an apparent threat posture. No specimens of *E. fusiforme* or *E. serriferum* have been seen to do this.

E. gracile does well in aquaria, specimens having been kept for several months on a diet of white worms, pieces of earthworms, frozen brine shrimp, and moistened pellets of dry food. Linder (1955a) also reported success in maintaining *E. gracile* in aquaria.

Distribution—Found along the Gulf Coastal Plain from the Tombigbee River in Mississippi west to the Nueces River of Texas and northward in the low lying areas of the former Mississippi Embayment (Fig. 5). Hubbs (1957b:98) reported *E. gracile* as occupying the Texan, Austroriparian, and Tamulipan biotic provinces of Texas, but absent from the Rio Grande drainage of the Tamulipan. In northeastern Oklahoma, Blair (1959) noted that *E. gracile* is found mostly in the sluggish, turbid streams of the Cherokee Prairie biotic province avoiding the clear, faster flowing streams of the Ozark biotic province. In Indiana it is known only from the lowland southwest corner south of the Wisconsin glaciat (Gerking, 1945:95, map 94).

There is only one collection of *E. gra* available from the Tombigbee Ri (UMMZ 113453, Lowndes Co., Miss.). *zoniferum* has been taken several tir farther south in this river. These two very similar to each other, so much so t I think they would probably hybridize they came together. *E. zoniferum* is clea an offshoot of *E. gracile,* and so they wo not be expected to be in the same ri system together. Therefore, there is a p sibility that a stream capture allowed *gracile* to invade the upper part of Tombigbee River. Tributaries of three (ferent rivers approach this section of Tombigbee; the Yalobusha, tributary to Yazoo, the Big Black, and the Pearl. T tributary of the Big Black is the one t approaches closest to the Lowndes Cou locality and also there are more collecti of *E. gracile* from it than from the other t rivers.

A better understanding of factors imp tant in the distribution of *E. gracile* can obtained by study of a limited area. Illin was selected because Forbes and Richard (1920) gave a lengthy account of the pography of the state, and because it been well covered by collectors (IN UMMZ, CU). All known Illinois locali for *E. gracile* were plotted upon a map glacial geology taken from Forbes and R ardson (1920, Map III). The collecti they reported as *Boleichthys fusiformis* fr the Rock River district of northeast Illin refer to the superficially similar *Etheosto exile,* as pointed out by Hubbs and Can (1935). The distribution of *E. gracile* Illinois is listed below: (names from For and Richardson, 1920:Atlas):

Drainage system	*No. collecti*
Galena District, Rock River System, Lake Michigan Drainage, Mississippi Drainage	n
Illinois River System	
Kaskaskia River System	
Wabash River System	
Big Muddy River System	
Saline River System	
Cairo District	

Only two collections of *E. gracile* are f the Illinois River, which drains about th

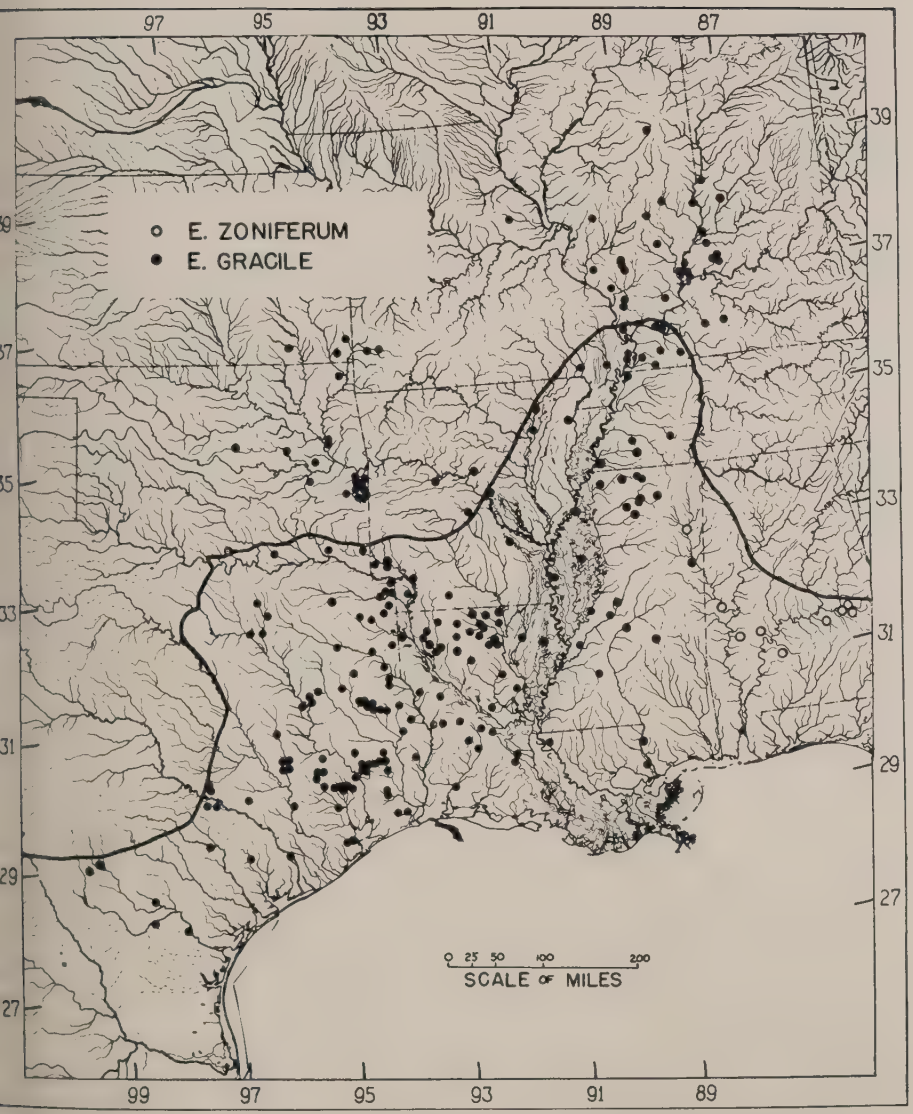


Figure 5. The distribution of *Etheostoma gracile* and *E. zoniferum* in relation to the Fall Line. (Based upon specimens examined)

sevenths of the state. This seems odd because the whole state has been covered thoroughly by collectors. Each collection is represented by only a single specimen. I have verified the identification of the Champaign Co. specimen and although the Christian Co. specimen appears to be lost (P. W. Smith, personal communication), it was examined by Hubbs and Cannon so its actual identification is not suspect. The Champaign Co. specimen was mentioned in Thompson's field notes but no specimens have been taken in more recent collections (P. W. Smith, personal communication);

therefore there is a possibility that the locality for the Christian Co. specimen is erroneous.

With the exception of the two abovementioned specimens and a specimen from a Madison Co. tributary of the Kaskaskia River, the remainder of the *E. gracile* collections are from only three of the nine physiographic areas of Illinois (Forbes and Richardson, 1920, Map III):

	No. collections
1) Unglaciated areas (of southern Illinois only)	6
2) Lower Illinoisan Glaciation	18
3) Bottom lands (of Lower Illinoisan Glaciation only)	36

The two Illinois River specimens came from the Wisconsin and Middle Illinoisan Glaciation area and the Madison Co. specimen came from the Middle Illinoisan Glaciation. Concerning the drainage of Illinois, Forbes (1909:381) pointed out that "... the headwaters and tributaries of its various stream systems so approach and intermingle that in times of flood they formed an interlacing network, through which it would seem that a wandering fish might have found its way in almost any direction and to almost any place." Why then is *E. gracile* so clearly limited to the southern part of the state? The answer lies in the glacial geology which, as Forbes (1909) pointed out, is more diversified than the topography. The Kaskaskia and Embarrass Rivers cut across the Shelbyville moraine which separates the lower Illinoisan and Wisconsin glaciations, but the distribution of *E. gracile* stops south of the moraine, although the bottomlands which are its preferred habitat continue across the moraine into the Wisconsin Glaciation for a short distance. Two physical factors seem important in limiting *E. gracile* distribution: current and turbidity.

Forbes (1909) presented a list of seven species tolerant of muddy bottoms and a list of thirteen species that avoid muddy bottoms. All the species in the former group are freely distributed over the lower Illinoisan Glaciation and all the species in the latter group avoid this area. The streams of the Wisconsin Glaciation are narrow and fast flowing, quickly carrying off any silt load they acquire. Forbes and Richardson (1920) also pointed out that the soil the lower Illinoisan Glaciation is an tremely fine-grained, light-colored which when washed into streams rema in suspension and renders the waters tur for a long time. The correlation of tur waters and muddy bottoms with *E. gra* distribution seems to be due not to a pref ence of *gracile* for this type of habitat to the fact that more species of fishes present in the favorable upland habitat have become specialized for certain ecolo cal niches. They are therefore able to co pete more successfully which leaves the m dy swamps by default to *gracile* and ot fishes tolerant of poor conditions.

I have computed the gradient in feet mile for streams in which *E. gracile* was lected, basing my calculations on the d of Forbes and Richardson (1920) and L (1933). In ten streams, the most upstre collection of *gracile* was found in areas h ing gradients of 1.0 to 6.7 feet per m ($\bar{x}$:2.9 ft/mi). The gradients that *gra* avoids in these streams range up to 100 mi ($\bar{x}$:18.3). Of course, most *gracile* w collected in backwaters and so were fou at gradients of much less than 2.9 ft/ It seems that the upstream spread of *gra* is limited by fast water in the same way t the Atlantic Coast species of the subge *Hololepis* are limited by the Fall Line.

In Illinois and Indiana a number of s cies have distributions similar to that of *gracile*. Gunning and Lewis (1955) no that *Lepomis symmetricus, Elassoma zo tum, Chologaster agassizi, Gambusia a. finis,* and *Centrarchus macropterus* h their northern limit in southern Illin Four species are limited to the extre southwestern tip of Indiana, in the area the Wabash River and Ohio River fl plain (Gerking, 1945): *Gambusia a. affi Centrarchus macropterus,* and *Etheosto chlorosomum,* in addition to *Etheosto gracile.* Of twenty species of darters which Gerking (1945) presented distri tion maps, only *E. gracile* and *E. chloro mum* are limited to the southwest cor of the state. *Opsopoeodus emiliae* also the center of its Indiana distribution in muddy waters of the southwestern cor of the state.

Geographic Variation—Tables 10-16 g frequency distributions of the charact

examined and include *E. zoniferum;* this facilitates comparison between these closely related species. Several characters which showed little or no geographic variation are given only in the species comparisons tables (Tables 38-49); squamation of interorbital, parietal, and breast (naked); condition of preopercle (entire); coronal pore (present); interorbital pores (usually absent, rarely 1-2); pectoral rays (mode usually 13, a few populations with 12); branchiostegals (usually 6, Mississippi to Missouri population with a mode of 5).

The number of pored and total lateral-line scales showed little difference between populations (Tables 10-11). The modal number of dorsal spines was nine in all populations except for an Audrain Co., Mo. collection (UMMZ 149331) which had a mode of ten (Table 12). The modal number of second dorsal rays is 11 in all populations except Missouri to Ohio and Colorado, which have 12 (Table 12). A spine was present in the anterior part of the second dorsal fin more often in *E. gracile* (13 specimens) than in the other species of the subgenus *Hololepis*. Most specimens of *E. gracile* had two anal spines but 22 specimens had only one spine and one specimen had three (Table 42). The modal number for anal rays was either six or seven (Table 13).

By use of the number of scale rows above the lateral line (Table 14), populations of *gracile* may be divided into three groups: Populations east of the Mississippi with a low number (mode of three); the Mississippi, Vermilion, and Calcasieu populations with a moderate number (modes three or four); and a western group from the Sabine through the Nueces, with means greater than 3.75 (except for the Brazos) and a mode of four. In regard to the number of scale rows below the lateral line (Table 14) the Nueces population stands out with a mean of 9.73. The other populations had means from 8.5 to 9.0, with the exception of the Trinity population, which was intermediate with a mean of 9.46.

There were no important differences between populations in the number of head pores. Most specimens had ten preoperculomandibular pores but some individuals had as few as eight or as many as 11 (Table 15). Two anomalous specimens had incomplete POM canals (Missouri-Ohio and Neches systems). Both had counts of 5 + 6, and therefore would have had normal counts of ten if the canal had been complete. The infraorbital pores are typically eight (Table 15) but range from six to ten. The INF canal is typically complete but two individuals had 3 + 5 (Red River) and 2 + 6 (Missouri-Ohio drainage). Both of these would be low counts of seven if the canals were complete. The supratemporal canal is usually complete in adults but in most collections a few specimens had incomplete canals (see development).

The preopercle (POP) and opercle (OP) are completely covered with scales but the character of squamation varies (Table 16). Most specimens had POP covered with exposed ctenoid scales (X-T) but a few had the squamation less well developed. One Sabine River specimen had imbedded cycloid scales and the sample had a mode of PX/X-T. The OP squamation was similar but less well developed. The mode is usually X-T but it varied to I/PX-T in the Wabash population. The extent of the nape that was covered by scales varied from 0-100% within many populations, but the mode was usually 100 I/PX-T (Table 16).

The most interesting result of comparison of populations of *E. gracile* is that although there is a large amount of variation within systems and within collections as in *E. fusiforme,* there is much less difference between populations. This is probably due to less complete isolation, than in fishes living along the Atlantic Coastal Plain.

Specimens Examined—Specimens examined are given by drainage system, state, county, and museum number, except for localities at the margins of the range and type localities of nominal species. A total of 1580 specimens from 309 collections was examined. Complete data for most of the collections are listed in Collette (1960).

Tombigbee Dr., Miss.—Lowndes Co.: UMMZ 113453 (10, 28-36); Tombigbee R., 3 mi. W of Columbus: Aug. 18, 1931.

Pascagoula Dr., Miss.—Newton Co.: CU 33795 (1, 33); trib. of Leaf R. between Lawrence and Lake on US 80; Oct. 25, 1958.

Pearl Dr., Miss.—Pearl River Co.: TU 14423 (1, 30); oxbow of W. Pearl R., 3.2 mi. E of Bogalusa, La.; Nov. 11, 1956. Rankin Co.: USNM 129113 (25, 13-21); borrow pits on Meeks Ferry Rd. along Pearl R.; June 12, 1933. La.—St. Tammany Par.: UMMZ 163687 (1, 40); ditch 1 mi. E of Pearl R. village; Apr. 15, 1951.

Mississippi River

Ohio-Wabash Dr., 40 specimens. Ind.—Gibson Co.: UMMZ 81382. Green Co.: USNM 34983 (1, 31); Switz City Swamp; Aug. 1883; lectotype of

Poecilichthys palustris. Knox Co.: UI 425. Posey Co.: UI 446. Ill.—Crawford Co.: INHS uncat. Cumberland Co.: CU 34586. Effingham Co.: UMMZ 105940. Wayne Co.: INHS uncat. White Co.: CU 32245; TU 19326.

Ohio Dr., 44 specimens, Ind.—Warrick Co.: UMMZ 81406; UI 440, 441; CU 32246. Ky.—Muhlenberg Co.: CU 22186.

Wabash to Mississippi Dr., 38 specimens, Ill.—Massac Co.: INHS 4 uncat. coll.; TU 35155. Saline Co.: INHS uncat. Ky.—Hopkins Co.: USNM 63782. Marshall Co.: UMMZ 168360.

Middle Mississippi

To Missouri Dr., 17 specimens, Ill.—Champaign Co.: INHS uncat. Mo.—Audrain Co.: UMMZ 149331.

Missouri to Ohio Dr., 63 specimen, Ill.—Alexander Co.: UMMZ 111594. Bond Co.: CU 34587. Jackson Co.: UMMZ 107048, 105930. Jefferson Co.: UMMZ 105866, 163066. Madison Co.: UMMZ 131198. Perry Co.: UMMZ 130301. Randolph Co.: UMMZ 163079. Union Co.: CU 3466. Washington Co.: UMMZ 163027.

Ohio-Arkansas Dr., 45 specimens, Ark.—Craighead Co.: USNM 125086. Ky.—Graves Co.: USNM 63783; TU 3018. Hickman Co.: UMMZ 154781. Miss.—Coahoma Co.: USNM 129185. Mo.—Butler Co.: UMMZ 139647. Mississippi Co.: UMMZ 153260, 153237, 153201. New Madrid Co.: UMMZ 153159. Tenn.—Chester Co.: UMMZ 168526. Haywood Co.: UMMZ 161034. Obion Co.: UMMZ 105396; CU 33346. Shelby Co.: USNM 195973.

Lower Mississippi

Yazoo-Big Black Dr., 35 specimens, Miss. — Benton Co.: UMMZ 161444, 162897; UM H51-2, Copiah Co.: UMMZ 170715. De Soto Co.: USNM 129013, 129593. Hinds Co.: UMMZ 170744. Holmes Co.: UMMZ 161108. Lafayette Co.: UMMZ 161392, 162923; UM 50-6, 51-19, 55-4. Marshall Co.: UMMZ 161054; UM 51-2, 55-16. Sunflower Co.: USNM 170978. Union Co.: UMMZ 144722. Warren Co.: USNM 129110. Washington Co.: USNM 129123. Yazoo Co.: USNM 32224 (1, 44); Vaughan's Station, pool along Big Black R., Aug. 20, 1881; holotype of *Poecilichthys butlerianus;* USNM 129140.

Arkansas Dr., 169 specimens, Mo.—Barton Co.: UMMZ 151793. 151815. Ark.—Arkansas Co.: TU 2196. Faulkner Co.: Univ. Ark. uncat. coll. Jackson Co.: UMMZ 123620. Lawrence Co.: USNM 109881. Pulaski Co.: UMMZ 123262. Yell Co.: TU 24466. Okla.—Craig Co.: OAM 5172. Le Flore Co.: UMMZ 109427; OAM 972, 1001, 1136, 1234, 1090, 782, 1182. 1319, 1343, 1357, 1403, 1390, 4473. Lincoln Co.: OAM 4529. McIntosh Co.: TU 10559. Muskogee Co.: OAM 4329, 5054. Okmulgee Co.: UMMZ 107052. Osage Co.: OAM uncat. Ottawa Co.: OAM 5147. Pittsburg Co.: OAM 4961. Kans.—Cherokee Co.: UMMZ 144463 (2, 29-30); Fly Cr., 4 mi. S and 3 mi. W of Hoover at Columbus; July 26, 1946. Crawford Co.: UK 2255 (6, 29-36); Clear Cr. and Second Cow Cr., Sec. 20, T29S, R24E; Apr. 18, 1952. UK 2933 (4, 31-34); Cow Cr., Sec. 20, T29S, R24E; Apr. 10, 1953. Montgomery Co.: UK 6043 (1, 43); Big Elk Cr. between Independence and Elk City on US 160; Mar. 28, 1961.

Red-Ouachita Dr., 717 specimens, Ark.—Columbia Co.: USNM 165848. Hempstead Co.: UMMZ 123169. Howard Co.: TU 10165. Lincoln Co.: UMMZ 127832. Little River Co.: UMMZ 170868. Miller Co.: UMMZ 123135, 123125. Saline Co.: USNM 36470. Sevier Co.: TU 10165. La.—Bienville Par.: UMMZ 170824; USNM 172878. Bossier Par.: UMMZ 170842; USNM 172608, 172661, 172883, 173002. Caddo Par.: CU 32249, 32248. Caldwell Par.: TU 14372. Catahoula Par.: TU 4343. Claibourne Par.: UMMZ 161294. Grant Par.: TU 907, 2096, 4296. Jackson and Bienville par.: USNM 172576. Lincoln Par.: UMMZ 161310; USNM 172495, 172623, 172523, 172745, 172889, 172934. Madison Par.: USNM 172732. Natchitoches Par.: TU 13649. Ouachita Par.: UMMZ 170780, 170804; USNM 172762. St. Landry Par.: TU 961, 1021. Union Par.: TU 14355; USNM 172481, 172560, 172570, 172677, 172692, 172709, 172812, 172833, 172861, 172911, 172953. Webster Par.: TU 1355; USNM 172648, 172988. Okla.—Bryan Co.: OAM 4192. Choctaw Co.: OAM 2108, 4684. Love Co.: OAM 4766. McCurtain Co.: UK 2418; OAM 2165, 3074, 3004, 5169; CU 17890, 33746. Tex.—Bowie Co.: OAM uncs TNHC 3529, 3930, 4992. Bowie and Cass co TNHC 3179. Cass Co.: TNHC 3508, 3542, 39 4044, 4092. Franklin Co.: TU 14070. Harri Co.: TNHC 2048. Morris Co.: TNHC 3845. River Co.: TNHC 4994.

Calcasieu Dr., 6 specimens; La.—Allen Pa USNM 172116; TU 14050. Calcasieu Par.: AN 55538. Vernon Par.: UMMZ 170594; TU 14090

Sabine Dr., 34 specimens; La.—Sabine Pa TU 976, 4564. Vernon Par.: TU 14360. Tex Harrison-Panola cos.: TNHC 3217. Newton C TNHC 3300. Panola Co.: CU 34909. Sabine C TNHC 465. Shelby Co.: TNHC 3387. Shel Panola cos.: TNHC 3591. Upshur-Smith co UMMZ 170038.

Neches Dr., 129 specimens, Tex.—Cherokee C TNHC 3809. Hardin Co.: TNHC 488, 578; 21651, 22214, 21417. Nacogdoches Co.: UM 170469; TNHC 363, 371, 202, 400, 1061, 12 1776, 556; TU 14037. Polk Co.: UMMZ 1704 TNHC 2419, 2575, 2696. Rusk Co.: CU 345 Sabine Co.: UMMZ 170502. San Augusti Nacogdoches cos.: UMMZ 170480. Tyler C TNHC 2943; TU 14085, 21373, 21464, 217 21845.

Sabine Lake Dr. (Neches plus Sabine), 4 sp mens, Tex. — Jefferson Co.: TNHC 4181; 22295.

Trinity Dr., 44 specimens, Tex.—Anderson C TU 3801. Collin Co.: TNHC 3434, 3739. Fr stone Co.: CU 33819. Kaufman Co.: TNHC 40 Madison-Walker cos.: TU 4899. Polk Co.: TN 509, 1345, 1601, 2029, 2720, 2757. San Jaci Co.: UMMZ 170429.

San Jacinto-Galveston Bay Dr., 68 specime Tex.—Harris Co.: UMMZ 86325, 170399, 1588 Liberty Co.: TNHC 1587. Montgomery C UMMZ 147541; TNHC 1165, 1394, 1146, 12 1219, 1476, 1517, 2004, 2957; TU 14065. Wal Co.: TNHC 1006, 1793, 2750.

Brazos Dr., 23 specimens, Tex.—Brazos C UMMZ 129938, 129863, 129804, 129749. Robe son Co.: CU 33333. Waller Co.: TNHC 4267

Colorado Dr., 52 specimens, Tex.—Bastrop C TNHC 1890, 3715, 3796, 5272. Lee Co.: TN 2541. Wharton Co.: UMMZ 170310.

Navidad Dr., Tex.—Lavaca Co.: TNHC 1 (1, 40); Navidad R., 2 mi. NW Seclusion; M 5, 1951.

Guadalupe Dr., Tex.—Gonzales Co.: USI 166171 (16, 22-41); Guadalupe R., L. Belmo 2 mi. above Wrights Camp; Apr. 17, 1952.

Nueces Dr., Tex.—Live Oak Co.: Lake Cor Christi State Park. TNHC 4975 (1, 37); F 1954 and TNHC 4974 (1, 41); Dec. 11, 19 McMullen Co.: TNHC 1766 (6, 34-38); Nue R., 10 mi. W Sutton; Dec. 6, 1947. TNHC 3 (1, 38); 8.6 mi. N Tilden, San Miguel Cr.; J 15, 1952. Uvalde Co.: USNM 1328 (1, 36); totype and MCZ 113 (1, 36); paratype; Rio S near Ft. Inge; and USNM 1329 (1, 31); Le R. near Ft. Inge; paratype of *Boleosoma grac*

Etheostoma zoniferum (Hubbs and Cannon)

Hololepis zonifer—Hubbs and Cann 1935; 47-50, pl. I-III (original description Fowler, 1945: 40 (Ala. R. after Hubbs a Cannon).

Etheostoma zoniferum—Bailey and G line, 1955:20, 44 (number of vertebrae Eddy, 1947:219; Moore, 1957:198; Co 1959:35, 200, 208 (Miss.); Collette, 196 2051.

Types—Holotype, UMMZ 88803, 31 m female; Ala., Pools of Catoma Cr., 5 SW of Montgomery; Sept. 18, 1929; Crea and Becker. Paratype, UMMZ 88822; A Lowndes Co.; Pools of Big Swamp Cr.,

mi. SW of Montgomery; Sept. 18, 1929; Creaser and Becker.

Diagnosis—*E. zoniferum* differs from its close relative *E. gracile* primarily in having the infraorbital canal incomplete with 2+4 pores. It also has fewer anal rays (mode: 6, $\bar{x}$:5.9), fewer scale rows above the lateral line (mode: 3, $\bar{x}$:3.2) and below the lateral line (mode: 8, $\bar{x}$:8.2). Maximum size of males—36.6 mm and females 35.0 mm (Tombigbee R., UMMZ 163758).

Coloration—No specimens of non-breeding adult males or females were available. The patterns of breeding *E. zoniferum* are like those of breeding *E. gracile;* the patterns of the non-breeding individuals are probably also similar. The pattern of the non-breeding female *zoniferum* is probably like that of the breeding female *zoniferum,* as is usual in the subgenus *Hololepis.*

There are a few scattered medium-sized melanophores on the first dorsal fin membranes in the breeding female. Small melanophores are concentrated on the distal portions of the posterior membranes. The second dorsal rays are barred and large melanophores are scattered on the membranes, especially on the basal eighth of the fin. Melanophores outline the anal rays, and a few are present on the posterior membranes. The pectoral rays also are outlined. The pelvic fin is clear. The caudal fin is barred. The breast and belly are immaculate, with a few melanophores sometimes present posteriorly on the belly. Large melanophores are scattered on the cheek. All four orbital bars are present; the suborbital is the most prominent; the supraorbital extends onto the eye. The pored portion of the lateral line stands out as a narrow light line, but pigment is sometimes present on the distal margin of the pored scales. The median basi-caudal spot is prominent and indistinct spots are present at the upper and lower bases of the caudal fin. The sides are brown with blotches more or less apparent. The dorsal saddles are indistinct. The genital papilla is unpigmented. Figure 4 compares the patterns of breeding females of *E. zoniferum* and *gracile.*

The pectoral and caudal fins, basi-caudal spots, dorsal body surface, and genital papilla in the breeding male are colored like the respective parts of breeding females; other areas are darker. Melanophores are concentrated in the lower two-thirds of the first dorsal fin except for a narrow light basal area. The barring of the rays of the second dorsal fin is somewhat obscured by the greatly increased number of melanophores on the membranes. The anal and pelvic fins and the belly and breast are uniformly covered with small melanophores. The suborbital bar appears less distinct in the male because the cheek is darker. There is more pigment on the posterior portions of the pored lateral-line scales than in the female. The sides are more uniformly brown. The patterns of breeding males of *E. zoniferum* and *gracile* are compared in Figure 4.

In life, *E. zoniferum* is quite colorful. R. M. Bailey's field notes on UMMZ 158228 described the male as having a sub-terminal orange band on the first dorsal. The top of the head was a greenish-olive. The lower fins were white. The back was cream-colored and barred with brownish-grey. The lateral bands were greyish-blue.

Carl L. Hubbs' field notes on UMMZ 163758 described the male as having red spots forming a series along the light streak in the first dorsal fin. The red was rather indistinct forward and stronger posteriorly, and the spots were smaller posteriorly. There was a trace of these marks in the female. The first dorsal fin of the male was sooty. The body of the male had deep metallic blue-green lateral bars. The color has completely faded out in the preserved specimens.

Genital Papilla.—The genital papilla in the breeding female is like that of *E. gracile* (Fig. 1c).

Breeding Tubercles—Tubercles are present on the anal fin rays and on the rami of the lower jaw. None have been seen on the pelvic fin rays, probably because of lack of material taken at the height of the breeding season. A few small tubercles are present on the distal parts of the anal fin rays, especially on the distal third of the third ray. In a 38 mm male taken on April 16 (UMMZ 163758) from the Tombigbee River, there are four low tubercles in a row on the ramus of the right half of the lower jaw but none are discernible on the left half. This incomplete development of the jaw tubercles is taken as further evidence that the tubercles of this specimen either

have not reached, or are past, maximum development. The distribution of tubercles on the chin and anal fin is like that in *E. gracile* (Fig. 1h, m).

Development—There is little information on the change of characters with age in *E. zoniferum*. The supratemporal canal seems to show the same changes as in *E. fusiforme*. Eight specimens smaller than 25.9 mm had incomplete supratemporal canals, sixteen between 26.0 and 29.9 mm were equally divided between complete and incomplete, and the five available specimens 30.0 mm and larger had complete canals. None of the available specimens were small enough to detect any other changes with age.

Habitat—Hubbs and Cannon (1935) described the habitat at the first two localities from which the species was known as pools in creek bed; water: clear, murky; bottom: gravel, mud; depth to four feet; vegetation: sparse *Chara;* temperature: moderate, warm.

Distribution—Found only in the Alabama and Tombigbee Rivers below the Fall Line (Fig. 5). I do not know why it is not distributed still farther south in these two river systems. Both *E. gracile* and *zoniferum* have been taken in the Tombigbee River in the state of Mississippi. Further collecting is desired in order to find out if they occur together.

Geographic Variation—Tables 10-16 compare the Alabama and Tombigbee populations of *E. zoniferum* with the populations of *E. gracile*. On the basis of the small samples now available, there seem to be no differences between the populations of the two rivers. Tables 38-49 compare *E. zoniferum* with the other species of the subgenus *Hololepis*.

Specimens Examined—Alabama R., Ala.—Macon Co.: UMMZ 111223 (2, 22-23); 3 mi. E of Tuskegee; June 3, 1931. UMMZ 124012 (14,24-28) and USNM 117546 (1, 27); Slough Lake, Tuskegee, East Opintoloco Cr., Sept. 13, 1937. UMMZ 124020 (2, 30-34); Big Swamp, Tuskegee; Sept. 13, 1937. API 566 (2, 26); Slough Lake, SE of Tuskegee, Opintoloco Cr.; Sept. 13, 1937. API 567 (1, 37); Watering Br., Tuskegee; Oct. 3, 1939. Montgomery Co.: UMMZ 88803 (1, 30); pools of Catoma Cr., 5 mi. SW of Montgomery; Sept. 18, 1929; holotype of *Hololepis zonifer*. UMMZ 158228 (1, 27); cr. 19 mi. SE of Montgomery on US 231; Sept. 4, 1939. Wilcox Co.: UAIC 526 (1, 26); Chilatchee Cr. near Alberta; Aug. 30, 1956. UAIC 536 (1, 29); Prairie Cr., 13 mi. E of Camden and 0.5 mi. W of Oak Hill near Ala. 10; Aug. 30, 1956.

Tombigbee R., Ala.—Marengo Co.: UAIC 428 (1, 28); Beaver Cr., 10 mi. SW of Linden (near Ala. 79 and 10 mi. N of jct with Ala. 10); Aug. 24, 1954. Greene Co.: UMMZ 163758 (2, 35-37); flood pool in Tombigbee R., 2½ mi. E of Epes; April 16, 1941. Miss.—Monroe C UMMZ 157751 (1, 28); Tombigbee R., 2½ W of Amory; Aug. 16, 1939.

Etheostoma fusiforme fusiforme (Girard)

Boleosoma fusiforme—Girard, 1854: (original description).

Hololepis fusiformis—Putnam, 186: (original description of *Hololepis* by Ag siz); Cope, 1864:233 (diagnosis of the s cies of *Hololepis*); Greeley, 1939:43 (Lo Island, N. Y.); Webster, 1942:127, 196, 2 (Pataganset Lake, Conn.); Cronk, 195((Long Island); Everhart, 1950:43-44 (Mc Raney, 1950:177-178, 186, 190 (James Va.); Smith, 1950: (fish fauna of N. lakes and ponds); Smith, 1953a: (N. J Smith, 1953b:168 (acidwater fishes southern N. J.); Stroud, 1955:7, 353 (An Long Pd., Mass.); Fletcher, 1957:202-2 (N. J. specimens spawned in aquarium Mullan and Tompkins, 1959:132.

Hololepis erochrous—Cope, 1864:2 (original description); Fowler, 1940: (Bucks Co., Pa.); Fowler, 1952:124 (loc ity records, N. J.).

Boleichthys fusiformis—Smith, 1907:2(268 (in part, N. C.); Fowler, 1911: (ecology, Del.); Schrenkeisen, 1938:2 (brief description); Fowler, 1935:6 (part, general distribution); Driver, 19 285 (in key, in part); Driver, 1950:2 (in key).

Copelandellus quiescens—Smith, 19(268-269 (in part, ecology and spawni N. C.).

Hololepis fusiformis erochrous—Hub and Cannon, 1935:72-77, pl. I, III (descr tion, range, synonymy); Mansueti, 19 301-302 (ecology, Md.); Harmic, 1952: (Del.); Mansueti and Elser, 1953:1 (ecology, Chambers Lake, Md.); Tru 1953:1 (in Md. pond after rotenone app cation).

Hololepis fusiformis atraquae—Hubbs a and Cannon, 1935:68-72, pl. I, III (origi description); Fowler, 1945:40 (Potom R.).

Hololepis fusiformis insulae—Hubbs a Cannon, 1935:83-86, pl. I, III (origi description).

Hololepis fusiformis metae-gadi.—Hub and Cannon, 1935:81-86, pl. I, III (origi description).

Hololepis fusiformis fusiformis—Hubbs nd Cannon, 1935:77-81, pl. I, III (descrip-on, range, synonymy); Gordon, 1937:102, 16 (N. H.); Bailey, 1938:150-151, 156-61, 176-177, 183 (Merrimack River water-hed, N. H.); Bailey and Oliver, 1939:152, 79, fig. 78 (N. H.); Cooper, 1939:55 Me.); Carpenter and Siegler, 1947:77 N.H.); Harrington, 1947:191 (fry in . H.).

Hololepis thermophilus—Hubbs and Can-on, 1935:63-67, pl. I, III (original descrip-on); Fowler, 1945:40 (Neuse R.); Frey, 951:9, 37-41 (N. C. Bay Lakes).

Hololepis thermophilus thermophilus—ailey and Frey, 1951:191-204, pl. 1-8 comparison with *H. thermophilus oligo-orus*).

Hololepis thermophilus oligoporus—Bail-y and Frey, 1951:191-204, pl. 1-8 (original escription).

Etheostoma fusiforme fusiforme—Bailey nd Gosline, 1955:20, 44 (number of ver-brae); Collette, 1961:2051.

Etheostoma fusiforme erochroum—Bailey nd Gosline, 1955:20, 44 (number of ver-brae).

Etheostoma fusiformis—Smith, 1957: (N.), 125-126 (food of *Esox niger*).

Etheostoma thermophilum—Moore, 1957: 98.

Etheostoma fusiforme—Eddy, 1957:219, 22, fig. 546; Moore, 1957:198; Collette, 958:77 (ecology, Me.); Behnke and Wet-el, 1960:143 (Conn.).

Etheostoma barratti—Eddy, 1957:220 range, in part); Knapp, 1953-128 (range, part).

Types—Hubbs and Cannon (1935) se-cted USNM 1188, a 33 mm female, as e lectotype from a series of syntypes USNM 94686) collected by S. F. Baird in tributary of the Charles River at Framing-am, Mass. Other paratypes of the same iginal lot are MCZ 24589 (4 specimens) nd UMMZ 86582 (1 specimen).

Diagnosis—Distinguished from the other ecies of the subgenus *Hololepis* by a com-nation of the following characters: two nal spines; interorbital pores absent; usu-ly nine preoperculomandibular pores; in-aorbital canal incomplete; breast entirely aled. Distinguished from *E. f. barratti* by e following: preopercle usually entire 0% of specimens examined); infraorbital usually 2 + 3 (80%); fewer interorbital scales (0-12, $\bar{x}$:2.0); parietal less completely scaled (usually 0-20%, $\bar{x}$:9.5%). Maximum size of males 44.1 mm, females 49.3 mm (CU 33194, N. Y., Suffolk Co., Lower Lake Yaphank).

Coloration—The patterns in this form are extremely variable. Much of this variation is associated with the color of the water from which the specimens were taken, darker stained waters generally produce darker fish, etc. The following description is based upon "typical" specimens and the most common variations from the "typical" pattern.

In the female small melanophores are concentrated on the posterior edge of the first dorsal spines and a few scattered melanophores may be present at the base of the membranes. Some large melanophores are scattered over the membranes of the second dorsal fin. The anal rays are barred; some specimens have a few melanophores on the membranes. The pelvic rays bear a few scattered melanophores. The pectoral and caudal fins are barred. The belly and breast vary from being immaculate to having scattered melanophores. The cheek has a few scattered large melanophores. All four orbital bars are present; the suborbital is usually the most prominent; the supraorbital extends onto the eye and the suborbital sometimes does so. The pored portion of the lateral line appears as a narrow light line which is interrupted by some pigment underneath the scales. There is usually a prominent black basi-caudal spot just below the center of the caudal base; the dorsal and ventral basi-caudal spots are usually faint. The sides have 8-13 indistinct dark brown or black blotches below the lateral line, which tend to fuse into a dark lateral band. Some specimens, especially from New Jersey and Delaware, have this lateral band exceptionally prominent in contrast to the upper part of the body which is a light tan. Approximately 12 dorsal saddles alternate with the lateral blotches in some specimens. The genital papilla is usually unpigmented, but small melanophores often encircle the anal region. Figure 6 compares breeding females from five localities.

In the non-breeding male the pectoral, pelvic, and caudal fins, orbital bars, basi-caudal spots, genital papilla and dorsal body

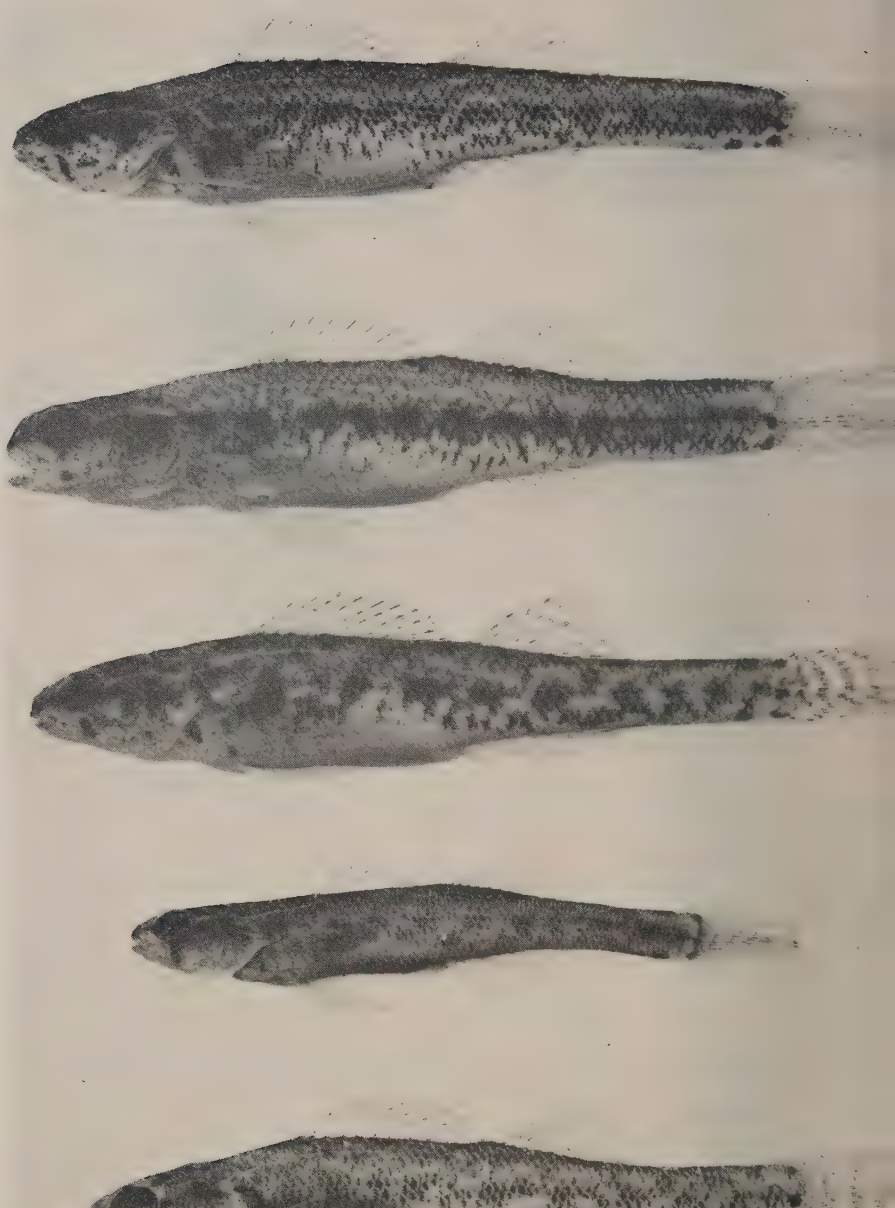


Figure 6. Breeding patterns of female *Etheostoma fusiforme fusiforme*. (from to bottom) CU 31847; 38.5 mm; N.Y., Suffolk Co., Lake Yaphank; Apr. 19, 1958. 32725; 38.0 mm; N.J., Atlantic Co., Great Egg Harbor dr.; May 16, 1959. CU 31 37.9 mm; N.C., Northampton Co., Roanoke dr.; Apr. 4, 1958. CU 25304; 28.4 N.C., Bladen Co., Jones Lake; Aug. 24-26, 1947. CU 14302; 35.7 mm; N.C., Colun Co., Waccamaw dr.; Mar. 29, 1949. (Photograph by Douglass M. Payne)

rface are colored like the female; the her areas are darker. The dorsal and anal ns have varying numbers of melanophores attered on the membranes. The belly and east range from immaculate to being cov-ed with small melanophores. The cheek darker than that of the female. The nar-w light line is interrupted more than it in the females. Most non-breeding males nd to have the body more uniformly pig-ented, obscuring the lateral blotches.

In the breeding male the pectoral and udal fins, pored portion of the lateral line, nsi-caudal spots, genital papilla, and dorsal ody surface all have the same melanophore stribution as the non-breeding male; other gions are darker. The large number of elanophores present on the dorsal fins alesce, in specimens from some localities, d form a solid black band (Fig. 7). The gmentation is most intense on the first ree or four interspinous membranes. The al and pelvic fins have large melanophores attered over their membranes; these are ually more prominent on the anal. The eek, belly, and breast are much darker than the female and non-breeding male. The des are similar to the non-breeding male, t with lateral blotches obscure in some ecimens. Figure 7 shows the pigment pat-rn of breeding males from five localities.

Genital Papilla—In the breeding female, e genital papilla is an elongate tube with slit opening on the anterior side (Fig. 1f). he papilla is a conical tube either with or ithout a bulbous enlargement similar to at usually present in *E. gracile* (Fig. 1h). he tip is more pointed than in the other ecies of the subgenus *Hololepis*.

Breeding Tubercles—Present on the anal ys (similar to *E. gracile,* Fig. 1j) and on e undersides of the pelvic rays (Fig. 1k). hey seem to be less developed in *E. fusi-rme fusiforme* than in *E. f. barratti,* and e present for a shorter time. Tubercles ve been found on specimens from only urteen collections and in some series, small bercles were present on only one or two ecimens. This may be because most col-ctions were either made before or after e spawning season. In the southern part the range, tubercles have been found on: arch 25 (Ellis Lake, CU 29983); March and 29 (Waccamaw R., DU B-49-12 and U 14302); April 4 (Roanoke R., CU 31640); and March 27 (Chowan R., CU 16880). Tubercles have been found on specimens from a number of New Jersey collections made on May 17 and 18, 1958 and 1959 (CU 31083, 32739, 31797, 31787, 31791, 31794, 32744). One specimen taken on March 27 in Lake Yaphank, N. Y., (CU 31850) had tubercles on the anal fin while most males in an April 19 collection (CU 31847) had tubercles on both anal and pelvic fins.

Development—Two characters clearly change with age in *E. fusiforme fusiforme:* the condition of the supratemporal canal and the number of pored lateral-line scales. The supratemporal canal is incomplete in young and juveniles and normally becomes complete by maturity. Table 31 shows the development of this character in a number of *E. fusiforme* populations. The Long Island population may be taken as an example of normal development. In young specimens the supratemporal canal extends only part way up the side of the head, with the two sides of the canal widely separated. The two sides grow toward each other until they join and the only vestige of the former separation is the central pore. All Long Island specimens up to 21 mm have the supratemporal canal incomplete. Some specimens from 21-25 mm have the supratemporal canal complete and others incomplete. Those 25 mm and larger have complete supratemporal canals (incomplete canals in only four adults). The situation is more complex in the North Carolina Bay Lakes and will be discussed under geographic variation, supratemporal canal.

The second character that changes with age is the squamation. As in *Perca flavescens* (Pycha and Smith, 1955), *Micropterus dolomieui* (Everhart, 1949:113) and *Pomoxis nigromaculatus* (Ward and Leonard, 1954), scales first appear on the caudal peduncle at the base of the caudal fin. Later they extend forward along the lateral line and then spread dorsally and ventrally. Sixteen larvae (9.1-11.1 mm) taken on May 16 and 17, 1958 in New Jersey (CU 32725 and CU 32739) completely lack scales. Four specimens (13.3-14.9 mm) from Lake Ronkonkoma, N. Y., taken on July 6, 1956 (CU 30279) also lacked scales. Two specimens (13.4 mm) taken from Lake Ronkonkoma on Aug. 3, 1956 (CU 30347) had

TABLE 18.

Number of total lateral-line scales in Etheostoma fusiforme

Drainage	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	N	$\bar{x}$	SD	SE
f. fusiforme																												
Ogunquit						1	2	2	—	—	2	3	1	1											12	49.08	2.71	.25
Cape Neddick							1	2	3	1	3	3	1	1	—	1									16	49.75	2.41	.19
North-Isinglass											1	2													3	50.67	—	—
Merrimack					1	1	8	6	6	13	13	15	8	7	10	5	1								94	50.39	2.73	.28
Ipswich								4	5	7	5	5	5	1	1	—	1								34	49.97	2.12	.36
Mass. Bay									1	4	7	3	3	5	2	—	1	—	1						27	51.48	2.33	.45
Neponset								2	3	1	5	4	3	—	2	2									22	50.68	2.38	.51
North R.								1	1	—	3	2	1	1											9	50.22	1.86	.62
Mills R.					2	3	3	9	20	17	10	10	4	1	2										81	48.84	2.03	.23
other Cape Cod							1	1	6	12	12	17	21	26	21	5	11	1	2	1	1				138	52.34	2.50	.21
Nantucket		1	1	2	1	3	2	3	2	2															17	44.71	2.59	.63
Wewcantic R.					1	1	3	3	4	2	2	1	1	2											20	48.35	2.54	.60
Taunton R.					1	1	1	—	—	2	2	12	5	6	3	1	—	1							35	51.34	2.57	.43
Seekonk							1	1	—	4	2	7	5	4	1	1									26	51.04	2.05	.40
[illegible]																												
Neuse							2	2	6	8	9	9	3	7	—	2	1								49	16.37	2.26	.32
Ellis L.				1	2	2	3	3	4	6	12	8	2	3	—	2									48	13.31	1.94	.28
Singletary L.		3	1	3	3	6	5	7	7	4	5	4	1												53	10.19	3.45	.47
Salters L.	3	3	2	3	2	3	8	9	9	5	5	1	1	1											55	7.42	3.11	.42
Jones L.	11	4	8	6	4	8	15	6	14	11	10	5	3	1	—	—	1								107	6.14	3.64	.35
White L.			1	—	—	—	1	1	—	3	5	12	23	37	26	51	45	39	21	22	14	6	5	2	2	—	1								317	15.54	3.08	.17
other Cape Fear								1	—	2	2	4	3	3	7	2	1				2	1												28	14.07	3.04	.57
Waccamaw				1	—	1	1	2	11	11	9	6	15	6	5	—	—	1																69	14.38	2.43	.29
f. barratti																												
Pee Dee									1	1	3	4	9	3	5	6	7	1	5	1	—	1			47	19.98	2.88	.42
Santee					1	—	—	—	1	3	7	11	4	9	7	1	6	7	3	4	1	2			67	17.66	3.50	.43
Edisto													1	2	1	2	2	1	2	2	1	1			16	20.25	3.00	.75
Combahee-Broad		1	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	1	4	2	1	—	1	1	13	19.69	6.05	1.68
Savannah							1	1	—	4	5	9	6	14	15	17	14	19	13	15	11	16	12	6	6	7	3	1	2	3	—	1	1	202	22.68	4.82	.34
Ogeechee											1	—	—	1	—	2	2	2	3	3	5	—	2	2	—	1	—	—	—	1	—	—	1	26	24.46	4.61	.91
Altamaha-Satilla													1	1	5	4	8	8	2	8	2	—	—	1	—	2								42	24.14	2.82	.43
St. Marys										1	3	1	1	5	2	2	4	3	8	1	3	1	2											37	22.89	3.50	.58
St. Johns										2	6	6	9	11	9	10	13	5	4	9	7	4	1	2	2	1	—	1						102	22.68	3.88	.38
St. Cloud	1	—	—	1	—	1	—	—	3	4	2	3	3	10	4	3	2	1																38	13.42	3.77	.61
Orlando		2	2	1	2	2	1	1	2	1	7	3	5	2	8	4	3	10	4	5	12	4	4	3	—	4	3	—	1	—	—	1					97	16.76	6.46	.66
Oklawaha-St. Johns							1	—	—	—	2	1	—	4	5	4	2	4	5	1	6	5	4	4	4	1	—	1	1						55	21.33	4.67	.63
Okeechobee				1	—	1	2	2	—	1	1	2	2	4	4	3	4	1	3	4	3	2	—	—	3	1	—	—	1						45	17.33	5.68	.85
S. Fla.													1	1	1	2	3	6	1	4	3	3												25	21.58	2.48	.50
Tampa Bay															1	1	2	1	4	1	2	4	4	—	—	1	—	1						22	24.68	3.17	.68
Withlacoochee-Waccasassa											2	1	2	4	—	3	—	1	2	1	2	1	—	1	—	—	1							21	20.90	4.42	.97
Newman L.											1	1	2	2	1	6	6	6	6	4	12	5	7	4	6	3	1	—	—	—	—	—	1	74	24.24	4.05	.47
other Suwannee											1	—	—	1	—	1	1	5	5	1	2	1	1												19	22.41	2.73	.63
Crystal L.	4	—	2	2	—	—	—	2	2	1	3	—	—	—	1	—	1																		18	6.06	4.86	1.14
Okefenokee													1	1	3	2	2	3	7	5	7	6	3	7	2	4	—	3						56	24.05	3.62	.48
Fenholloway-St. Marks										1	1	1	1	—	1	8	3	2	2	1	2	2	—	1	—	2								28	19.71	4.02	.76
Ochlockonee										1	1	1	1	—	3	8	10	12	10	7	9	5	12	5	3	1	2	—	—	—	1				92	21.74	3.61	.38
Apalachicola											2	2	3	5	6	3	2	3	3	3	5	—	—	1											38	21.50	3.30	.54
Choctawhatchee-Perdido										3	1	2	5	3	4	4	2	2	2	2	1	1	1											33	19.45	3.47	.61
Mobile Bay										1	1	2	1	—	—	—	1	1	1																8	19.00	3.46	1.22
Miss. Sound										1	—	—	1	—	1	2	—	—	—	—	1														6	19.17	—	—
Pearl-Pontchartrain									2	—	5	3	2	6	4	3	6	2	3	3	1														40	19.07	3.19	.50
Yazoo						1																													1	9	—	—
Reelfoot L.										1	—	—	—	1																					2	16.50	—	—
Red					1	—	—	—	3	3	3	6	8	4	—	4	—	1																		33	16.39	2.56	.45
French Broad							2	2	1	4	3	14	3	1	6	2	4	3	1																46	17.96	3.04	.45

TABLE 20.
Number of first dorsal spines in Etheostoma fusiforme

ainage	8	9	10	11	12	13	x̄
usiforme							
Ogunquit		2	9	–	1		10.00
Cape Neddick		2	3	1			9.83
North-Isinglass		3					9.00
Merrimack		15	53	26	1		10.14
Ipswich		12	18	4			9.76
Mass. Bay		2	20	3	2		10.19
Neponset		3	16	3			10.00
North		2	6	1			9.89
Mills		1	5	6			10.42
other Cape Cod	5	49	66	16	2		9.72
Nantucket	12	4					8.25
Weweantic		14	6	1			9.38
Taunton		9	21	5			9.89
Seekonk		7	19	1			9.78
Pataganset L.		5	8				9.62
Ronkonkoma L.		4	36	10	1		10.16
Yaphank L.		13	19	1			9.64
Raritan	8	21	19	7			9.45
Coastal N. J.	4	34	62	19	2		9.84
Delaware		10	33	15	1		10.12
Coastal Del.-Md.			2	4			10.67
Chesapeake Bay		8	47	20			10.16
Potomac		2	14	1			9.94
James			14				10.00
Nansemond	1	8	3				9.17
Chowan			11	68	34	2	11.23
Roanoke	1	27	46	7	1		9.76
Neuse		13	27	8			9.90
Ellis L.		26	28	3			9.60
Singletary L.	12	23	8				8.91
Salters L.	14	20	2				8.67
Jones L.	12	27	6				8.87
White L.	4	28	29	4			9.51
other Cape Fear		9	10	2			9.67
Waccamaw	3	18	27	15			9.86
barratti							
Pee Dee	1	13	23	11	1		9.96
Santee	2	13	42	11	1		9.94
Edisto		1	13	2			10.06
Combahee-Broad			10	4			10.29
Savannah		13	123	64			10.26
Ogeechee	2	2	12	10	1		10.22
Altamaha-Satilla		1	17	15	1		10.47
St. Marys		2	14	11			10.33
St. Johns		6	23	7	1		10.08
St. Cloud		9	24	6			9.92
Orlando		2	14	3			10.05
Oklawaha-St. Johns	2	7	28	12			10.02
Okeechobee	1	12	24	3			9.73
S. Fla.		2	10	3			10.07
Tampa Bay		7	7	2			9.69
Withlacoochee-Waccasassa			15	7			10.32
Newnan L.		3	14	9			10.23
Suwannee		1	15	3			10.11
Crystal L.	1	4	7	3			9.80
Okefenokee		4	29	19			10.29
Fenholloway-St. Marks	1	1	17	11			10.27
Ochlockonee		4	33	22	1		10.33
Apalachicola		2	15	9	2		10.39
Choctawhatchee-Perdido		5	15	14	2		10.36
Mobile Bay		2	4	2			10.00
Miss. Sound			6	1			10.14
Pearl-Pontchartrain		9	14	6	1		9.97
Reelfoot L.		1	–	1			10.00
Red			10	14	1		10.64
French Broad	2	15	27	3			9.66

TABLE 21.
Number of second dorsal rays in Etheostoma fusiforme

Drainage	8	9	10	11	12	13	
f. fusiforme							
Ogunquit			5	7			10
Cape Neddick			2	4			10
North-Isinglass				3			11
Merrimack		7	42	39	7		10
Ipswich			20	12	1		10
Mass. Bay	1	–	15	11			10
Neponset			7	15			10
North			4	5			10
Mills			4	5	3		10
other Cape Cod		1	27	83	25	2	11
Nantucket			4	3	1		10
Weweantic			3	9	9		11
Taunton			16	18	1		10
Seekonk			6	18	3		10
Pataganset L.			9	4			10
Ronkonkoma L.			5	31	12	2	11
Yaphank L.			1	16	16		11
Raritan		1	21	28	6		10
Coastal N. J.		1	26	67	25	2	11
Delaware		1	26	33			10
Coastal Del.-Md.			1	4	1		11
Chesapeake Bay			8	56	10	1	11
Potomac			3	12	2		10
James			6	7	1		10
Nansemond		1	7	3	1		10
Chowan		7	60	45	3		10
Roanoke			40	35	7		10
Neuse		1	19	24	4		10
Ellis L.		5	33	17	2		10
Singletary L.	1	9	24	9			9
Salters L.		1	17	17	1		10
Jones L.		13	27	5			9
White L.		5	43	17			10
other Cape Fear		1	4	16			10
Waccamaw		20	30	12			9
f. barratti							
Pee Dee	1	19	25	3	1		9
Santee			18	36	14	1	10
Edisto	1	4	10	1			9
Combahee-Broad		2	10	2			10
Savannah	1	10	58	91	40		10
Ogeechee			5	19	3		10
Altamaha-Satilla			6	22	5	1	11
St. Marys			11	15	1		10
St. Johns		1	11	21	4		10
St. Cloud		1	16	19	3		10
Orlando			10	8	1		10
Oklawaha-St. Johns			11	25	12	1	11
Okeechobee			15	14	10	1	10
S. Fla.			2	9	4		11
Tampa Bay		1	2	11	2		10
Withlacoochee-Waccasassa			3	10	8	1	11
Newnan L.		1	3	13	9		11
Suwannee			7	9	2	1	10
Crystal L.			6	9			10
Okefenokee			12	27	13		11
Fenholloway-St. Marks			5	13	11	1	11
Ochlockonee		1	28	27	3	1	10
Apalachicola			8	14	6		10
Choctawhatchee-Perdido			15	19	2		10
Mobile Bay			3	4	1		10
Miss. Sound			3	2	2		10
Pearl-Pontchartrain		1	10	15	3		10
Reelfoot L.			2				10
Red			4	16	5		11
French Broad			5	29	12	1	11

TABLE 22.
Number of scale rows above and below lateral line in Etheostoma fusiforme

	Above the lateral line						Below the lateral line									
Drainage	2	3	4	5	N	x̄	6	7	8	9	10	11	12	N	x̄	Total
f. fusiforme																
Ogunquit	3	9			12	2.75			6	6				12	8.50	11.25
Cape Neddick		5			5	3.00			1	3	2			6	9.17	12.17
North - Isinglass		3			3	3.00			2	1				3	8.33	11.33
Merrimack	8	87			95	2.92		4	50	32	6	1		93	8.46	11.38
Ipswich	13	20			33	2.61			22	12				34	8.35	10.96
Mass. Bay	1	26			27	2.96			11	16				27	8.59	11.55
Neponset	1	20	1		22	3.00			12	10				22	8.45	11.45
North		9			9	3.00		1	5	3				9	8.22	11.22
Mills		12			12	3.00			10	2				12	8.17	11.17
other Cape Cod	28	106	2		136	2.81		12	75	44	4	1		136	8.32	11.13
Nantucket	2	6			8	2.75		3	4	—	1			8	7.88	10.63
Weweantic	2	19			21	2.90		2	8	10				20	8.40	11.30
Taunton	7	28			35	2.80		1	22	11				34	8.29	11.09
Seekonk		26			26	3.00		1	16	7				24	8.25	11.25
Pataganset L.		13			13	3.00			11	2				13	8.15	11.15
Ronkonkoma L.	3	41	4		48	3.02			22	25	2			49	8.59	11.61
Yaphank L.		33			33	3.00			22	10	1			33	8.36	11.36
Raritan		49	7		56	3.13		7	38	11				56	8.07	11.20
coastal N. J.	13	102	2		117	2.91	1	24	58	29	3			115	8.08	10.99
Delaware	3	46	3		52	3.00		14	29	9	2			54	7.98	10.98
coastal Del. - Md.		4	1	1	6	3.50			3	2	—	—	1	6	9.00	12.50
Chesapeake Bay	1	59	12		72	3.15			11	54	9			74	8.97	12.12
Potomac	2	15			17	2.88			9	7	1			17	8.53	11.40
James	3	8	3		14	3.00		5	6	3				14	7.86	10.86
Nansemond	4	8			12	2.67		3	7	2				12	7.92	10.59
Chowan	42	67	5		114	2.68	2	43	56	11	1			113	7.70	10.38
Roanoke	19	62	1		82	2.78	3	29	46	2				80	7.59	10.37
Neuse	6	38	6		50	3.00		15	33	2				50	7.74	10.74
Ellis L.	36	21			57	2.37	10	45	2					57	6.86	9.23
Singletary L.	17	24	1		42	2.62		5	28	9				42	8.10	10.72
Salters L.	31	3			34	2.09	2	15	13	4				34	7.56	9.65
Jones L.	27	18			45	2.40		16	17	11	1			45	7.93	10.33
White L.	40	27			67	2.40		21	39	6	1			67	7.81	10.21
other Cape Fear	11	12			23	2.52	5	13	3	1	1			23	7.13	9.65
Waccamaw	42	21			63	2.33	6	23	29	5				63	7.52	9.85
f. barratti																
Pee Dee	14	27	5		46	2.80		1	20	19	6			46	8.65	11.45
Santee	17	49	2		68	2.78		5	34	22	7			68	8.46	11.24
Edisto		13	3		16	3.19			3	4	8	1		16	9.44	12.63
Combahee - Broad	3	10	1		14	2.86		1	6	6	1			14	8.50	11.36
Savannah	14	156	27		197	3.07		1	59	92	37	5		194	8.93	12.00
Ogeechee	2	23	2		27	3.00			6	11	9	—	1	27	9.22	12.22
Altamaha - Satilla		15	9		24	3.38		1	2	16	13	1		33	9.33	12.71
St. Marys	2	22	5		29	3.10			9	11	7			27	8.93	12.03
St. Johns	1	34	2		37	3.03		1	4	23	7	1		36	9.08	12.11
St. Cloud	20	19			39	2.49		11	25	3				39	7.79	10.28
Orlando	17	4			21	2.19	1	13	7					21	7.29	9.48
Oklawaha - St. Johns	7	40	2		49	2.90		3	11	25	8	1	1	49	8.92	11.82
Okeechobee	15	24	1		40	2.65		13	17	9				39	7.90	10.55
S. Fla.		10	5		15	3.33			5	8	2			15	8.80	12.13
Tampa Bay	1	18	3		22	3.09			6	9	7			22	9.05	12.14
With.-Waccasassa	2	13	2		17	3.00			6	7	3	1		17	8.94	11.94
Newnan L.	4	21			25	2.84			6	15	4			25	8.92	11.76
other Suwannee	3	14	1		18	2.89			3	10	6			19	9.16	12.05
Crystal L.	13	1			14	2.07		10	4					14	7.29	9.36
Okefenokee	2	44	5		51	3.06			16	29	5	1		51	8.82	11.88
Fenholloway - St. Marks	3	23	2		28	2.96			1	13	11	2		27	9.52	12.48
Ochlockonee	3	51	5		59	3.03			8	32	16	2		58	9.21	12.24
Apalachicola	3	20	5		28	3.07			5	13	7	2		27	9.22	12.29
Choctawhatchee - Perdido	2	27	5		34	3.09			9	16	6	4		35	9.14	12.23
Mobile Bay		7	1		8	3.13			1	7				8	8.88	12.01
Miss. Sound		7			7	3.00			1	4	1			6	9.00	12.00
Pearl - Pontchartrain	1	25	4		30	3.10			3	14	10	3		30	9.43	12.53
Reelfoot L.		2			2	3.00					1	1		2	10.50	13.50
Red	3	17	2		22	2.95			4	9	8			21	9.19	12.14
French Broad	5	40	1		46	2.91		1	5	29	10	1		46	9.11	12.02

TABLE 23.
Number of anal and pectoral rays in Etheostoma fusiforme

	Anal Rays							Pectoral Rays			
nage	5	6	7	8	9	10	$\bar{x}$	12	13	14	15
siforme											
gunquit		1	8	3			7.17				
ape Neddick		1	3	2			7.17				
orth-Isinglass		1	2				6.67				
errimack	3	27	52	13			6.79	1	4	1	
swich		10	21	3			6.79				
ass. Bay		2	15	10			7.30				
eponset		2	12	8			7.27				
orth		3	4	2			6.89				
ills			4	7	1		7.75		5	1	
ther Cape Cod		4	71	61	2		7.44		10	5	
antucket		2	3	3			7.13		4	4	
eweantic			8	11	2		7.71				
aunton		5	25	5			7.00	3	6		
eekonk		1	14	12			7.41				
ataganset L.		3	8	1	1		7.00		4	1	
onkonkoma L.			7	35	9		8.04		4	3	
aphank L.			10	13	10		8.00	1	14		
aritan		8	30	18			7.18		8		
oastal N. J.		15	53	43	10		7.40		9	3	1
elaware	1	14	31	13			6.95		5	1	
oastal Del.-Md.		2	2	2			7.00	1	5	2	
hesapeake Bay		2	39	32	2		7.45		10		
otomac		1	8	7	1		7.47	1	6		
ames			9	5			7.36		2	1	
ansemond			7	4	1		7.50		4	1	
howan		9	63	39	4		7.33		11	4	
oanoke		4	40	32	6		7.49		9	1	
euse		5	26	18	1		7.30		9	1	
llis L.			16	32	9		7.88				
ingletary L.			15	26	2		7.70		3	2	
alters L.			7	24	5		7.94		3	2	
ones L.		2	14	25	4		7.69	1	7		
White L.			22	41	2		7.69		4	3	
ther Cape Fear		1	14	7			7.27				
Waccamaw		2	33	24	3		7.45	1	9		
arratti											
Pee Dee	1	4	25	19			7.27		4	1	
Santee		1	20	38	9	1	7.84	1	9	2	
Edisto			2	12	2		8.00	2	6	1	
Combahee-Broad			3	7	4		8.07		7	2	
Savannah		20	55	90	35		7.70		10		
Ogeechee			6	17	4		7.93		4	1	
Altamaha-Satilla		5	16	9	4		7.35		5	4	1
St. Marys		1	9	17	1		7.64	1	5	1	
St. Johns			14	19	4		7.73	2	2	2	
St. Cloud		1	12	25	1		7.67				
Orlando		2	12	4	1		7.21				
Oklawaha-St. Johns		3	17	21	8		7.69				
Okeechobee			6	24	9	1	8.13		5		
S. Fla.			7	7	1		7.60	7	3		
Tampa Bay		1	5	8	2		7.69	1	3	1	
Withlacoochee-Waccasassa			9	9	4		7.77		3	2	
Newnan L.				9	17		8.65	1	3	1	
Suwannee			10	8	1		7.53	2	5	1	
Crystal L.			8	6	1		7.53			6	9
Okefenokee			17	32	3		7.73		8	1	1
Fenholloway-St. Marks		2	15	9	2		7.39	1	2	6	
Ochlockonee		4	44	12			7.13	1	7	7	
Apalachicola		5	18	4	1		7.04		5		
Choctawhatchee-Perdido		3	24	8			7.14	2	8	4	
Mobile Bay			3	5			7.63		2	2	
Miss. Sound		1	3	3			7.29	1	3	2	
Pearl-Pontchartrain		2	20	7	1		7.23	3	11	1	
Reelfoot L.		1	–	1			7.00		1		
Red		1	10	13	1		7.56	1	4		
French Broad			10	29	8		7.96				

scales along the posterior portion of the lateral line and in others (16.7 mm and larger) squamation is nearly complete. In the July 6 collection, squamation is nearly complete in specimens 15.6 mm and larger.

The pored lateral-line scales do not develop until after the body squamation is nearly complete. Figure 11 shows the change in number of pored lateral-line scales with age in the Long Island population. Small lateral ridges grow higher and higher and finally form the pore by meeting over the middle of the scale. The smallest (15.6 mm) *E. f. fusiforme* with a fully developed pored scale was taken from Lake Ronkonkoma (CU 30279) on July 6. The pored scales form quite rapidly starting at the anterior part of the lateral line. After about 20 mm there is little or no change in the number of pored scales (Fig. 11). The development is similar in White Lake, one of the North Carolina Bay Lakes (Fig. 12) but the dark Bay Lakes show a more complicated situation that will be discussed under geographic variation, pored lateral-line scales.

Habitat—E. fusiforme fusiforme is found primarily in ponds, swamps, and backwaters of streams. I have taken it only rarely in flowing waters, and then not in abundance. In many areas (*e.g.,* in New Jersey), mill ponds and ponds for cranberry bogs provide an ideal habitat for *E. f. fusiforme.* Mansueti (1951) found 1,000 specimens after rotenoning such a pond in Maryland.

The bottom at most *E. f. fusiforme* localities consists of mud or detritus. This is especially true in the realtively few collections in which both *Etheostoma olmstedi* and *E. f. fusiforme* were taken. For example, in Lower Lake Yaphank, Long Island, the southern end of the lake is mostly sand bottomed, with some areas of mud and detritus. Seining in the detritus produced only *E. f. fusiforme* and collecting over the open sand only *E. olmstedi.* Where both species were taken in streams *olmstedi* occupied the central sandy areas while *f. fusiforme* was limited to the weedy, mud-bottomed backwaters. However, in the absence of *olmstedi,* as in some of the acid water ponds of the New Jersey Pine Barrens, *f. fusiforme* may be quite abundant over open sand.

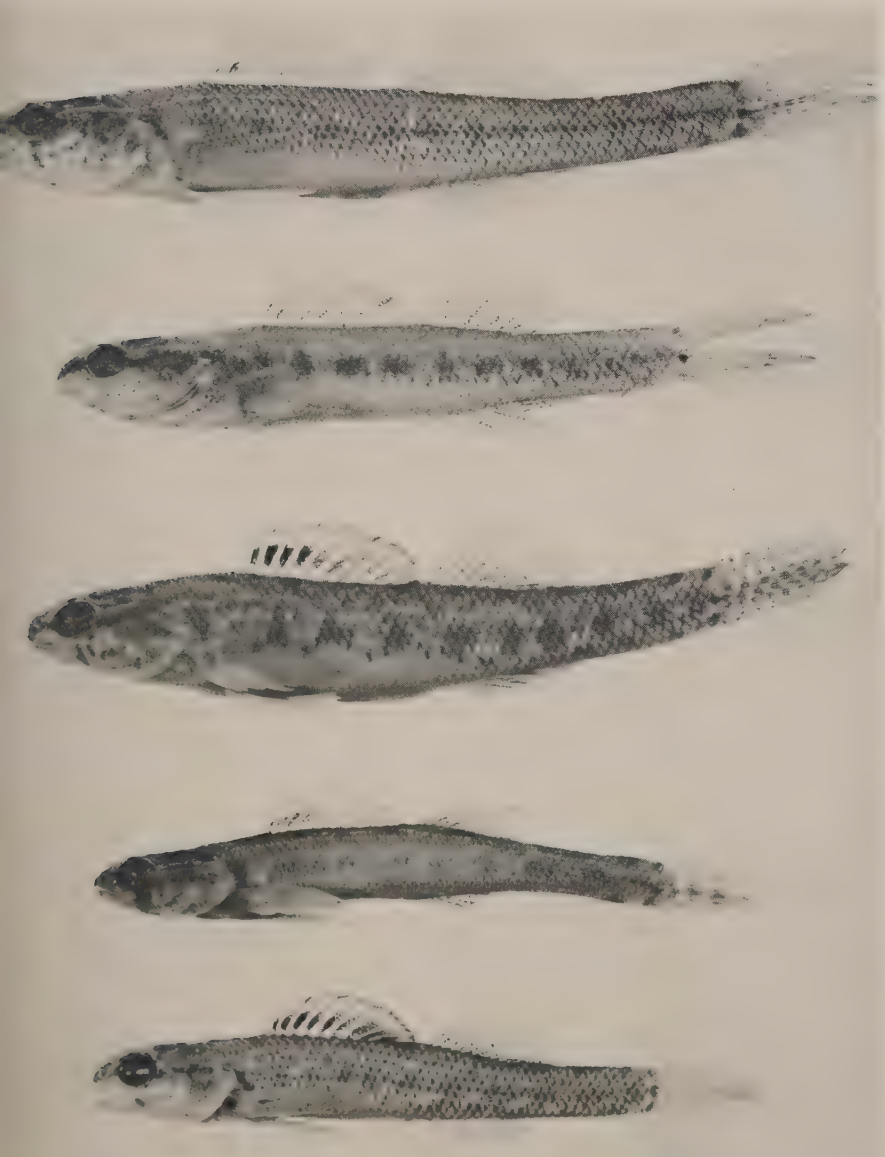
The body of *E. f. fusiforme* is quite compressed, adapted for living in dense aqua vegetation, while the heavier body of *olmstedi,* roughly triangular in cross secti is adapted for living on stream bottoms ing a current. A specimen of *E. f. fusifor* dislodged from its protecting weed bed the outlet stream of Wildwood Lake, L Island, was carried downstream by the rent, while *E. olmstedi* maintained its p tion on the bottom. *E. olmstedi* also pears to live in more highly oxygena waters than does *f. fusiforme.*

Although usually reported from brown-stained waters, *E. f. fusiforme* is limited to such habitats, but is found th for two reasons. It avoids currents, many of the slow waters on the Coa Plain are acid and brown-stained. Secon most fishes are poorly adapted to this t of habitat and the acid-water fishes species associates) avoid competition fr other species by living there.

In Maine, Everhart (1950) reported t *E. f. fusiforme* was "taken in sluggish, l land streams and mudholes among the ve tation" and Collette (1958) stated that "is usually found in muddy, swampy are In Delaware, Fowler (1911) noted that was "abundant in almost all lowland fr waters, at least above tide." Harmic (195 found that it was "abundant in mill po and sluggish waters" in Delaware. Mansu (1951) described four millponds and a sl gish stream in Maryland where it was tak In Connecticut, it has been reported fr Pataganset Lake, where it was found o muddy bottom among floating margi vegetation (Webster, 1942, and perso observation). In New Jersey, Smith (195 reported that it appeared to seek cover vegetation and detritus to a greater deg than the Johnny darter (*E. olmstedi*). Sm (1907:269) quoted W. P. Seal to the eff that around Wilmington, N. C., it will " stand warm and stagnant water better th any other darter I know of." This was a noted by Hubbs and Cannon (1935:6 who referred to a statement by G. S. My about *E. f. fusiforme* around Wilmingt N. C. "...it occurs abundantly in v warm, quiet waters reaching summer te peratures of 85° to 90°F. or even more, the depth of 3 or 4 inches in masses filamentous algae along banks of 'bl water' streams." Bailey (1938:176) see

TABLE 24.
Number of infraorbital pores and condition of the preopercle in Etheostoma fusiforme

Drainage	0+2	0+3	1+2	1+3	1+4	2+0	2+2	2+3	2+4	3+3	3+4	N	% 1+3 etc.	Condition of Preopercle PS	E	%PS
f. fusiforme																
Ogunquit				1	–	–	–	11				12	8.33	2	10	16.7
Cape Neddick								16				16	0	3	13	18.8
North - Isinglass								3				3	0	2	1	–
Merrimack								88	1	3		92	0	19	76	20.0
Ipswich				1	–	–	–	30	–	1		32	3.13	3	31	8.8
Mass. Bay				7	–	–	–	20				27	25.93	2	25	7.4
Neponset				2	–	–	–	20				22	9.09		22	0
North				1	–	–	–	8				9	11.11	2	7	22.2
Mills				13	–	–	–	47				60	21.67		62	0
other Cape Cod		1	–	19	–	–	–	111	4			135	14.81	10	128	7.2
Nantucket				2	–	–	–	15				17	11.76		19	0
Weweantic				2	–	–	–	18	–	1		21	9.52		21	0
Taunton				5	–	–	–	30				35	14.29	1	34	2.9
Seekonk		2	–	2	–	–	–	17				21	19.05		27	0
Pataganset L.				1	–	–	–	12				13	7.69		13	0
Ronkonkoma L.				6	–	–	–	43				49	12.24	2	49	3.9
Yaphank L.								33				33	0	1	32	3.0
Raritan				7	–	–	–	49				56	12.50	4	52	7.1
coastal N. J.		1	–	14	–	1	3	105				124	12.10	1	125	.1
Delaware				5	–	–	–	48	–	2		55	9.09	19	48	28.4
coastal Del. - Md.				4	1	–	–	51	–	1		57	8.77	13	45	22.4
Chesapeake Bay				2	–	–	1	74	–	4	1	82	2.44	24	65	27.0
Potomac				1	–	–	–	34				35	2.86	11	24	31.4
James				1	–	–	–	13	1			15	6.67	2	12	14.3
Nansemond				4	–	–	–	9				13	30.77		14	0
Chowan				3	1	–	–	110	–	1		115	3.48	13	102	11.3
Roanoke								97	–	1		98	0	15	84	15.2
Neuse				2	–	–	–	47	–	1		50	4.00	12	38	24.0
Ellis L.		1	–	26	–	–	–	30				57	47.37	5	52	8.8
Singletary L.		1	1	42	–	–	–	13				57	77.19	1	58	1.7
Salters L.				39	–	–	–	8				47	82.98	3	47	6.0
Jones L.		4	2	64	–	–	–	2				72	97.22	2	72	2.7
White L.	1	–	3	13	–	–	2	81	–	1		101	16.83		142	0
other Cape Fear				2	–	–	–	25				27	7.41	8	21	27.6
Waccamaw				7	–	–	–	62	2	3		74	9.46	16	55	22.5
f. barratti																
Pee Dee				44	–	–	–	5				49	89.80	18	31	36.7
Santee		5	–	53	–	–	–	8	1			67	86.57	25	43	36.8
Edisto				14	–	–	–	2				16	87.50	4	12	25.0
Combahee - Broad				11	–	–	–	–	–	1		12	91.67	3	11	21.4
Savannah		1	–	83	2	–	1	106	3			196	43.88	42	164	20.4
Ogeechee				2	–	–	–	25				27	7.41	20	8	71.4
Altamaha - Satilla				14	–	–	–	25	–	1		40	35.00	18	22	45.0
St. Marys		1	2	26	1	–	–	9				39	76.92	21	19	52.5
St. Johns			1	89	1	–	1	10	2	2		106	85.85	18	90	16.7
St. Cloud			1	37	–	–	–	1				39	97.44	1	38	2.6
Orlando		1	–	86	2	–	–	8				97	91.75	51	56	47.7
Oklawaha - St. Johns				50	1	–	–	5				56	91.07	18	38	32.1
Okeechobee		3	1	38	–	–	–	4				46	91.30	6	40	13.0
S. Fla.				19	–	–	–	1				20	95.00	5	15	25.0
Tampa Bay				14	–	–	–	8				22	63.64	11	11	50.0
Withlacoochee - Waccasassa		1	–	19	–	–	–	7				27	74.07	11	16	40.7
Newnan L.		1	–	58	4	–	–	12				75	84.00	24	52	31.6
other Suwannee				11	1	–	–	9				21	57.14	8	11	42.1
Crystal L.				24	–	–	–	2				26	92.31	1	25	3.8
Okefenokee			2	32	–	–	–	21				55	61.82	38	19	66.7
Fenholloway - St. Marks				16	–	–	–	14				30	53.33	19	11	63.3
Ochlockonee				66	1	–	1	34	1			103	65.05	53	50	51.5
Apalachicola				24	1	–	–	26	–	1		52	48.08	13	32	28.9
Choctawhatchee-Perdido		1	–	14	–	–	–	21				36	41.67	15	21	41.7
Mobile Bay				8								8	100.00	5	3	62.5
Miss. Sound				6	–	–	–	1				7	85.71	5	2	71.4
Pearl - Pontchartrain		2	–	38								40	100.00	24	17	58.5
Yazoo				1								1	100.00	1		–
Reelfoot L.				2								2	100.00		2	–
Red				41	1							42	100.00	7	35	16.7
French Broad		2	–	44								46	100.00	36	8	81.8



ure 7. Breeding patterns of male *Etheostoma fusiforme fusiforme*. (from top to tom) CU 31847; 41.3 mm; N.Y., Suffolk Co., Lake Yaphank; Apr. 19, 1958. CU 25; 33.6 mm; N.J., Atlantic Co., Great Egg Harbor dr.; May 16, 1959. CU 31640; 4 mm; N.C., Northampton Co., Roanoke dr.; April 4, 1958. CU 25304; 30.4 mm; N.C., Bladen Co., Jones Lake; Aug. 24-26, 1947. (past maximum breeding pattern). 14302; 30.3 mm; N.C., Columbus Co., Waccamaw dr.; Mar. 29, 1949. (Photograph Douglass M. Payne)

TABLE 25.
Squamation of the breast in Etheostoma fusiforme

Drainage	I-C	I/PX-C/T	PX-T	X/PX-T	X
f. fusiforme					
Ogunquit	5				
Cape Neddick	6				
Merrimack	4	1			
Ipswich	9				
Mass. Bay	5				
Neponset	5				
Mills R.	4	1			
Cape Cod	10	2			
Weweantic	5				
Taunton	6	1			
Pataganset L.	5	2			
Ronkonkoma L.	4				
Yaphank L.	15	3			
Raritan	8	3	1		
Coastal N. J.	7	3	1		
Delaware R.	8	1			
Del.-Md.	7	1			
Chesapeake	5				
Potomac		3	–	3	
James	2	2	3		
Nansemond	5				
Chowan	3	2	4	1	
Roanoke			3	4	
Neuse	7	3			
Ellis L.	4	5	1		
Singletary L.		1	1	2	
Jones L.	1	2	1	1	
White Lake	9	9	2	2	
Other Cape Fear	4	2			
Waccamaw	2	2	1	5	
f. barratti					
Pee Dee	1	1	6	1	
Santee		5	–	1	
Edisto		5	–	1	
Combahee-Broad	8	1			
Savannah	1	4	4	1	
Ogeechee		4	3	1	
Altamaha-Satilla	2	6	6	1	
St. Marys	3	7	1	2	
St. Johns	2	5	1	–	
Orlando		2	1	3	
Oklawaha-St. Johns		1	2		
Okeechobee			1	4	
S. Fla.		3	3		
Tampa Bay					
Withlacoochee-Waccasassa			2	2	
Newnan L.		5	4	–	
Suwannee	3	5			
Crystal L.	2	4			
Okefenokee		5			
Fenholloway-St. Marks		1	6	3	
Ochlockonee		5	–	1	
Apalachicola	1	5			
Choctawhatchee-Perdido		3	2		
Mobile Bay			2	–	
Miss. Sound			6		
Pearl-Pontchartrain			3	2	
Reelfoot L.			1		
Red					
French Broad		2	3	–	

TABLE 26.

etal squamation in Etheostoma fusiforme (percent of parietal covered with scales)

nage	0	5-10	15-20	25-30	35-40	45-50	55-60	65-70	75-80	85-95	100	x̄
siforme												
gunquit	6											0
ape Neddick	6											0
errimack	5											0
swich	9											0
ass. Bay	3	2										3.00
eponset	5											0
ills R.	1	4										6.00
ape Cod	11	1										.63
antucket	4											0
eweantic	3	2										3.00
aunton	4	3										3.29
ataganset L.	6	1										1.07
onkonkoma L.	6											0
aphank L.	7	10										4.41
aritan	10	3										1.73
oastal N. J.	2	4										5.00
elaware R.	4	7										4.77
el.-Md.	2	5	1									6.88
hesapeake	2	7	1									7.00
otomac	4	3										3.21
ames		1	4	3								20.00
ansemond		4	1									9.50
howan		5	4	1								13.50
oanoke			3	2	–	1						25.83
euse		9	1									8.50
llis L.		6	4									11.50
ingletary L.	5	16										5.71
alters L.		3										7.50
ones L.		1	8									16.39
White L.			5	9	2	2	1					29.61
Other Cape Fear		2	2									15.00
Waccamaw		2	9	2								17.50
urratti												
Pee Dee			1	3	3	5						37.50
Santee					2	5	2	1	2	1		56.73
Edisto			2	2	5							30.83
Combahee-Broad			2	1								20.83
Savannah				2	1	2	1	1	1	1	1	57.75
Ogeechee			1	1	2	1	2	1	1	1		51.50
Altamaha-Satilla			1	1	4	1	1	–	1	1		46.50
St. Marys		1	2	–	–	1	1	2	4	1		56.67
St. Johns						1	–	–	5	5		79.32
Orlando							4	2				63.33
Oklawaha-St. Johns									1	1		85.00
Okeechobee					3	1	–	–	1	3	1	63.67
S. Fla.					1	1	1	2	1			59.17
Tampa Bay									2	2	2	88.33
Withlacoochee-Waccasassa						2	–	–	3	1	1	73.57
Newnan L.							1	1	1	7		81.50
Suwannee			2	2	3	–	–	1				33.75
Crystal L.		1	–	2	1	–	1					31.50
Okefenokee					2	1	–	–	1	1		57.50
Fenholloway-St. Marks						1	–	3	3	3		74.50
Ochlockonee					1	1	–	–	2	1	1	71.25
Apalachicola					1	–	1	–	2	2		70.83
Choctawhatchee-Perdido						1	1	1	1			67.50
Mobile Bay			1	1	1							27.50
Miss. Sound			2	3	1							25.83
Pearl-Pontchartrain				2	3	3	1	3	2	2		56.25
Red										5		87.50
French Broad			1	1	2	1	2	1	2			50.50

TABLE 27.

Number of interorbital scales in Etheostoma fusiforme

Drainage	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31//37	$\bar{x}$
f. fusiforme																																	
Ogunquit		4	2																														1.33
Cape Neddick	6																																0
Merrimack	4	7																															.64
Ipswich	3	5	1																														.78
Mass. Bay	4	—	1																														.40
Neponset	3	2																															.60
North	2	3																															.40
Mills R.	3	2																															.40
Cape Cod	1	4	5	1																													1.55
Nantucket	3																																0
Weweantic	2	3																															.60
Taunton	1	4																															.80
Seekonk	1	3	1																														1.00
Pataganset L.	5	2																															.29
Ronkonkoma L.	4	1	2																														.71
Yaphank L.	4	3	7	4																													1.61
Raritan	9																																0
coastal N. J.	9	4	4																														.71
Delaware R.	6	3	1																														.50
Del.-Md.	1	2	2	1	1																												1.86
Chesapeake	1	6	4	1																													1.42
Potomac		4	1																														1.20
James		1	4																														1.80
Nansemond			3	2																													2.40
Chowan		1	5	2	1	1																											2.60
Roanoke			1	3	1	3	—	2	—	—	1	—	1																				5.50
Neuse				3	6	—	—	1																									4.00
Ellis L.			3	2	1	—	3	1																									4.10
Singletary L.	2	6	9	3																													1.65
Salters L.				2	—	—	—	—	—	1																							5.00
Jones L.	2	1	3	8	2	—	1																										2.65
White L.			2	5	7	2	2	1																									4.00
other Cape Fear		1	1	4	4	2	3																										3.93
Waccamaw L.			2	3	1	1	—	1	2																								4.50
f. barratti																																	
Pee Dee							1	—	—	1	2	3	2	—	1	3	2	1	—	1	—	1	—	—	—	—	—	-	—	—	—	1	14.58
Santee							1	—	1	—	—	2	—	—	2	3	—	—	—	—	1	—	—	1									13.82
Edisto						1	1	1	—	—	1	2	1	—	1	—	—	—	1														10.44
Combahee Broad						1	1																										5.50
Savannah						1	—	—	2	—	2	2	—	1	—	—	3	2	—	—	—	—	1	—	—	2							14.38
Ogeechee										1	2	2	—	1	1	1	1	1	—	1													13.18
Altamaha-Satilla						2	-	2	2	5	2	1	1	—	2	1	1	1															10.20
St. Marys										1	1	2	2	—	1	1	2	1	—	—	1												13.58
St. Johns											3	—	—	—	2	1	—	2	1	1	—	1											15.00
Orlando								1	—	2	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	1							14.33
Oklawaha St. Johns								1	—	1	—	—	1																				9.33
Okeechobee							1	1	2	1	2	1	—	—	1	—	—	—	1														10.10
S. Fla.													1	1	3	—	1																13.83
Tampa Bay									1	—	—	—	1	—	—	—	1	—	—	—	2	—	—	—	—	—	—	1					17.16
Withlacoochee Wacasassa							1	—	—	—	2	3	—	—	—	—	1	2															12.11
Newnan L.												1	1	—	3	1	—	—	3	—	1												15.40
other Suwannee					1	—	1	—	2	1	2	—	—	—	—	—	1																	8.88
Crystal L.		1	1	1	—	1	—	1																									3.60
Okefenokee														2	2	1	—	1															14.33
Fenholloway St. Marks										2	1	1	—	1		1	1	—		1	1	- -	1										14.40
Ochlockonee									3	2	-	1	3	1		-	1	4	1	1	2	1											14.20
Apalachicola									1	—	—	—	—	—	1	—	1	—	1	—	—	1	—	—	—	—	—	1						17.16
Choctawhatchee-Perdido								1	1	1	1	1	1	1	1	—	—	—	—	—	1	—	1											12.60
Mobile Bay									1	—	1	—	1																					10.00
Miss. Sound									1	—	1	1	—	—	—	—	—	1																11.50
Pearl-Pontchartrain										1	—	1	2	4	2	1	—	—	1	1	—	—	—	1	—	—	—	—	—	—	—	1		15.33
Reelfoot L.															1																			
Red														1	—	2	1	1	1	—	1	—	—	—	—	—	-	—	—	—	1		18.00
French Broad						1	-	1	—	—	3	1	2	1	—	—	—	—	—	- -	.		1											11.20

TABLE 28.

Characteristics of the North Carolina Bay Lakes (based in part on Frey, 1949)

Characters	Black	Jones	Salters	Singletary	White	Waccamaw	Used for Indices?
x̄ Secchi disc depth (ft.)	1.8	2.4	1.8	2.5	11+	4.4	Phys.-Chem.
x̄ color (p.p.m.)	182	297	299	168	10	160	No
x̄ depth (ft.)	5.3	6.1	6.9	7.0	7.5	7.6	No
maximum depth (ft.)	7.1	8.7	10.1	11.8	10.6	10.8	No
area (A.)	1418	224	315	572	1068	8938	No
volume ($yd.^3$)	12,197,700	707,100	3,520,200	6,495,300	12,844,100	109,964,800	No
maximum length (mi.)	2.11	.80	.94	1.49	1.81	5.3	No
length of shore line (mi.)	5.91	2.19	2.70	3.92	4.77	14.21	No
shore line development	1.12	1.05	1.09	1.17	1.04	1.07	No
pH	4.40	4.34	4.49	4.50	4.92	6.95	Phys.-Chem.
ml. N/44 H_2SO_4 per liter	1.9	3.0	3.2	2.4	1.6	9.2	Phys.-Chem.
pounds of fish per acre	0.33	2.30	6.37	5.76	53.07	31.37	Biological
number of fish species	10	13	14	15	21	35	Biological
amount of aquatic vegetation	none	none	none	very little	moderate	abundant	Biological

TABLE 29.

Comparison of physical-chemical and biological characters of the North Carolina Bay Lakes by ranking

	Physical-Chemical Factors				Biological Characters					x̄	%
	light penet.	pH	alk.	total	lbs/A fish	amt. aq. veg.	No. fish species	total	Total Index	Pored Scales	1+3 INF pores
Black	1.5	2	2	5.5	1	2	1	4	9.5	–	–
Jones	3	1	4	8.0	2	2	2	6	14.0	6.14	97.22
Salters	1.5	3.5	5	10.0	4	2	3	9	19.0	7.42	82.98
Singletary	4	3.5	3	10.5	3	4	4	11	21.5	10.19	77.19
White	6	5	1	12.0	6	5	5	16	28.0	15.54	16.83
Waccamaw	5	6	6	17.0	5	6	6	17	34.0	14.38	9.46

(1 = *least productive*, 2 = *next productive*, 6 = *most productive*).

to be the only author to report it from fast waters (Merrimack River, N. H.), as follows: "Where found in streams they usually seek the fastest waters and seclude themselves in clumps of aquatic vegetation.... In lakes they are found in protected coves provided with dense growths of aquatic vegetation." Hubbs and Cannon (1935) gave brief descriptions of the habitat for each of their subspecies of *E. fusiforme* which verify what has already been brought out concerning their habitat.

Species Associates—Etheostoma f. fusiforme is found over a large range; species associates, therefore, are discussed by regions. I have collected throughout the range of this form and in addition there are publis data for the Merrimack River of N Hampshire (Bailey, 1938) and for the la and ponds of New Jersey (Smith, 19 1953a, 1957).

Esox americanus, Enneacanthus obesus, Etheostoma f. fusiforme all have similar tributions in New Hampshire: lowland (313 feet), brown-stained waters with ve tation at least moderately thick (Bai 1938).

An acid-water fish fauna (Smith, 195 exists in the brown-stained waters of Pine Barrens of southern New Jersey. T is composed of *Umbra pygmaea, Ictalu natalis, Noturus gyrinus, Aphredoderus s*

TABLE 30.
Fishes of the North Carolina Bay Lakes and of Crystal Lake, Georgia

Lake	Black	Jones	Salters	Single-tary	White	Wacca-maw	Crystal
Index of Productivity	9.5	14.0	19.0	21.5	28.0	34.0	–
Species							
Esox americanus	x	x	x	x	x	x	x
Erimyzon succetta	x	x	x	x	x	x	x
Ictalurus natalis	x	x	x	x	x	x	
Noturus gyrinus	x	x	x	x	x	x	
Gambusia affinis	x	x	x	x	x	x	x
Aphredoderus sayanus	x		x	x	x	x	
Ennecanthus gloriosus	x	x	x	x	x	x	x
Centrarchus macropterus	x	x	x	x	x	x	
Chaenobryttus gulosus	x	x	x	x	x	x	x
Perca flavescens	x	x	x	x	x	x	
Esox niger		x	x	x	x	x	
Etheostoma fusiforme		x	x	x	x	x	x
Fundulus notti		x	x		x		x
Micropterus salmoides		x	x	x	x	x	x
Notropis chalybaeus				x	x	x	
Lepomis macrochirus				x	x	x	x
Amia calva					x	x	
Anguilla rostrata					x	x	
Lepomis auritus					x	x	
Mesogonistius chaetodon					x	x(?)	
Lepisosteus osseus						x	
Dorosoma cepedianum						x	
Erimyzon oblongus						x(?)	
Notemigonus crysoleucas						x	x
Notropis petersoni						x	
Cyprinus carpio						x	
Ictalurus catus						x	
Roccus americanus						x	
Lepomis gibbosus					x	x	
Lepomis punctatus						x	
Pomoxis nigromaculatus						x	
Acantharchus pomotis						x	
Elassoma zonatum						x	
Fundulus waccamensis						x	
Menidia extensa						x	
Etheostoma perlongum						x	
Notropis maculatus							x
Labidesthes sicculus							x
Lepomis marginatus							x
Totals	10	13	14	15	21	35	13

Acantharchus pomotis, Enneacanthus us, Mesogonistius chaetodon, and *Etheo- ia f. fusiforme.* For the most part these fishes found at altitudes of 300 feet or Smith (1953b) noted for *E. obesus* these fishes are found in these areas iuse competition from other species is tly reduced or eliminated. In clearer, e alkaline waters of southern New Jer- other species replace the acid-water es: *Ictalurus nebulosus* replaces *I. nata- Enneacanthus gloriosus* replaces *E. obe-* and *M. chaetodon; Etheostoma olmstedi* aces *E. f. fusiforme;* species of *Lepomis* ace *Acantharchus,* etc. There are also eral wide-ranging species in New Jersey, *Micropterus, s. salmoides* and *Esox niger* ch form part of both the acid-water and alkaline-water faunas.

mith (1957) reported a change in spe- composition (or at least abundance) seems to be correlated with a change pH. In 1952, when the pH of Lefferts e, New Jersey, was 6.8, *Fundulus di- anus* and *Notemigonus crysoleucas* were mmon throughout the lake and both *Ic- rus nebulosus* and *Lepomis gibbosus* e abundant but stunted. In August 1954, pH was down to 4.4 and *I. nebulosus L. gibbosus* had become less abundant. June 1955, when the pH was 4.1, *No- igonus, I. nebulosus,* and *L. gibbosus* e still less abundant, and *Enneacanthus sus* was taken for the first time. In a enone sample taken on August 6, 1956, *E. obesus* and 4 *Etheostoma f. fusiforme* e taken with only 4 *I. nebulosus,* 13 *temigonus,* 3 *L. gibbosus,* and 1 *Fundulus.* the same day I obtained the following 15 minutes seining: 32 *E. f. fusiforme, E. obesus,* 3 *L. gibbosus.* I believe that s is evidence for one of the few times t pH (or effects connected with pH, h as productivity) can be indicated as portant in determining species abundance.

Smith (1907:269) quoted a letter from l concerning the associates of *E. f. fusi- me* in the vicinity of Wilmington, N. C.: his species is . . . to be found . . . where ndulus, Gambusia, Heterandria, Umbra, ologaster, Elassoma, Aphredoderus,* and fishes abound." In New Hampshire, rrington (1946) reported that *E. f. fusi- me* was often found on the bottom hin an inch or two of foraging bridled shiners, *Notropis bifrenatus,* and that *Enneacanthus obesus* was occasionally found in its immediate vicinity. He also noted (p. 55) that when young *Notropis bifrenatus* first appear they are sometimes found in a chance association with small schools of chub sucker fry (*Erimyzon oblongus*), golden shiners (*Notemigonus crysoleucas*) and northern mud darters (*E. f. fusiforme*). In Delaware, Fowler (1911:13) reported *E. f. fusiforme* "to be usually associated with *Erimyzon, Aphredoderus, Enneacanthus, Mesogonistius* and similar fishes." *Etheostoma f. fusiforme* was taken in 8 of 17 of my collections on the Delmarva Peninsula. Common associates (with number of times taken with *E. f. fusiforme* and total number of times taken) are: *Aphredoderus sayanus* (7/8); *Lepomis gibbosus* (7/14); *Anguilla rostrata* (6/11); *Erimyzon oblongus* (5/8); *Enneacanthus gloriosus* (5/6); *E. obesus* (3/4); *Acantharchus pomotis* (4/4); *Notropis chalybaeus* (3/3); *Mesogonistius chaetodon* (2/2); and *Noturus gyrinus* (3/4).

Predators—Smith (1950) reported *Etheostoma f. fusiforme* from *Esox niger* stomachs in a number of acid southern New Jersey lakes: Lake Absegami, Colliers Mills, Farrington Lake, Hanover Lake, Union Lake, and Barnegat Pines Lake (1953a). He also (1957) presented a table of the food of *Esox niger* from lakes of different acidity for specimens under 6 inches and over 6 inches. *Etheostoma f. fusiforme* formed 25% of the food of the smaller *Esox* in very acid waters (pH 4.0-4.8), 15% in acid waters (pH 4.9-5.5), 2% in slightly acid waters (pH 5.6-6.9) and 0% at pH 7.0 and over. For the larger *Esox,* the figures were 12%, 13%, 2%, and 0% for pH 7.0 and over. Harrington (1946) reported *E. f. fusiforme* from the stomach of a 16-inch *Esox niger* from the Oyster River, New Hampshire.

Smith (1950) reported *E. f. fusiforme* from the stomachs of *Micropterus s. salmoides* (mostly young) in Colliers Mills, Farrington Lake, Parvin Lake, and Union Lake.

Parasites—The only report of parasitism for any species of the subgenus *Hololepis* is that of Harrington (1946) who found that *E. f. fusiforme* from the Oyster River of New Hampshire was heavily parasitized

by glochidia. I have also noted glochidia on a number of specimens.

Acanthocephalans were found with their proboscides imbedded in the stomachs of three *E. f. fusiforme* taken on Long Island (CU 31847). One specimen had two, another five, the third specimen had six, and a fourth specimen had none.

Habits—Specimens collected from Lake Ronkonkoma, Long Island, on April 21, 1956, and brought into the laboratory, began pre-spawning behavior almost at once, although none of the females were distended with eggs. There were two phases to this behavior. First, the male approached the female from the rear, mounted her, and began to "beat" her with his pelvic fins. Usually a female "accepted" this but a male so approached immediately moved away from such attentions. A few weeks later the second phase began; after the male started "beating" a female, she "led" him forward into floating plants at the top of the aquarium. With the male close alongside, she pointed her genital papilla forward and up into a mass of plants, and quivered. On a few occasions two males followed a single female. No fighting or display of territoriality was ever noted. Although no eggs were actually seen being laid, spawning is probably essentially the same in the wild. Fletcher (1957) reported similar behavior in specimens collected on March 27, 1957, in New Jersey. Spawning followed and continued for two days. The eggs were deposited singly on leaves of *Myriophyllum* and hatched in eight to ten days. Smith (1907) quoted Seal's observations on some specimens taken near Wilmington, N. C., which spawned on the underside of lilies and other plants in a small still-water aquarium.

My collections from New Jersey on May 17, 1958, in four lakes indicated that some specimens had partially completed spawning. Two collections made in the same areas on May 16 and 17, 1959, by N. R. Foster and J. S. Ramsey contained adults and postlarvae as small as 9 mm. A school of 20 to 30 postlarvae was taken by dipnet while free swimming at the surface in six inches to two feet of water over open sand. No other species were closely associated with them (personal communication and field notes of N. R. Foster). On July 6, 1956, I collected 24 young in Lake Ronkonkoma, Long Island, ranging from 13.3 to 22.0 m They were taken about 30 feet out in lake on an open sandy bottom, in wa four to five feet deep. Fletcher's (195 aquarium specimens were about this s ("3/4 inch") when two months old. H rington (1947) reported taking "very sm fry" of *E. f. fusiforme* on July 2 and 5, the Oyster River at Durham, New Ham shire.

Although no aging based on scale re ing has yet been done, there is evidence indicate that a large number, if not m *E. f. fusiforme* live only for one year. M Long Island collections show only one ma size class. On July 6, in Lake Ronkonko the 24 specimens which were taken w postlarvae. In November and April specimens taken in Lake Yaphank w adults.

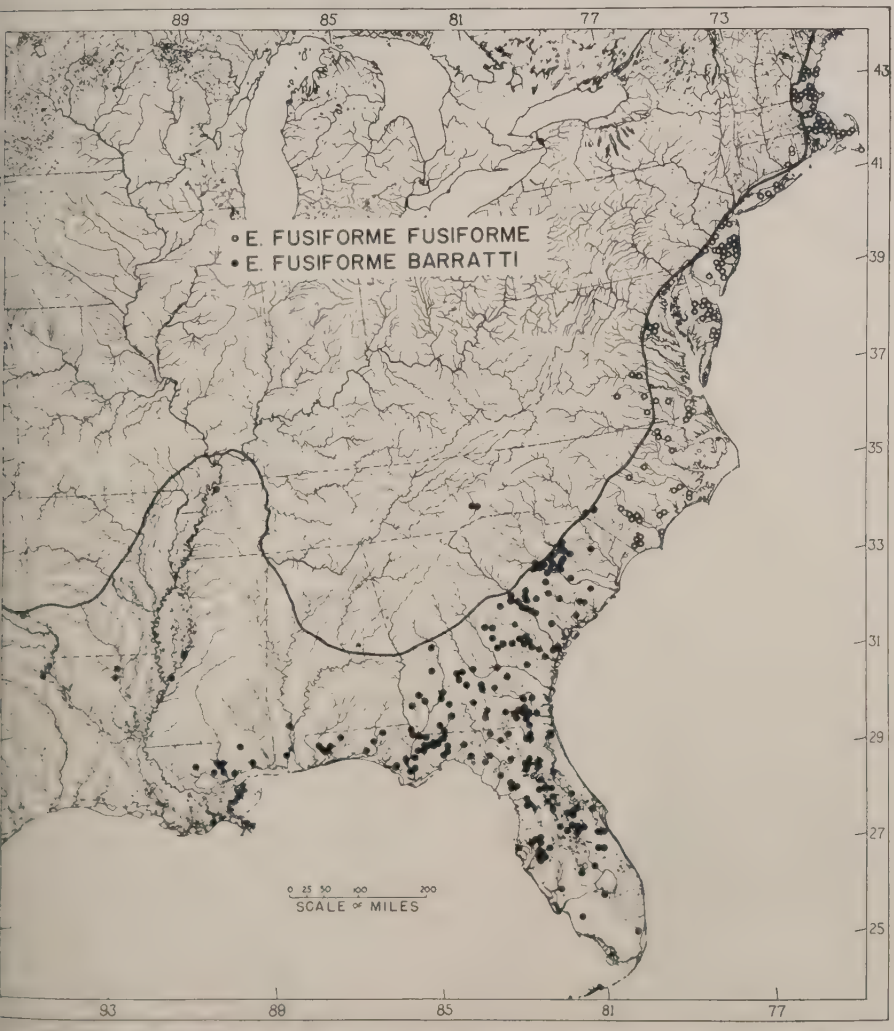
Everhart (1950) reported that you and adult *E. f. fusiforme* feed on entom traca in Maine. This is probably true, no food studies have yet been made of t subspecies. A 31 mm specimen from N Jersey had over 130 copepods in its stoma The intestine was filled with copepod e skeletons. A large number of specim from many localities had copepod exosk tons projecting from the anus. In aqua *E. f. fusiforme* feeds avidly on daph chasing them around the tank in spu They will also readily eat anything else small size that moves. Strange food is spected; the darter swims to the item, tu its head and looks down on the object w one eye. The object is then taken into mouth but rejected if not suitable. T have been trained to eat such non-liv food as frozen brine shrimp, frozen daph and dried fish food which has been dam ened and formed into small pellets. moderately large darters a supplement method of feeding was devised. A few p of guppies (*Lebistes reticulatus*) were ad to the tanks, and the darters fed on baby guppies.

A large number of specimens of *E. f. f forme* have been kept in aquaria. They easy to care for, interesting to watch, one of the easiest species of darter to tra port because of their apparently low oxy requirement. In aquaria, they spend m of their time either on the bottom among plants. Specimens often swim

a plant, such as *Elodea,* and balance themves there, with pectoral and pelvic fins in nt of the plant stem and the rest of the ly bent down behind.

Distribution—The range of *E. f. fusime* extends from the southeastern tip of ine along the Seaboard Lowland section the New England Province (Fenneman, 46) south along the Atlantic Coastal in below the Fall Line to the Waccamaw ver in North Carolina, south of which it replaced by *E. f. barratti* (Fig. 8).

The distribution of *E. f. fusiforme* in New Jersey has been analyzed to ascertain the factors important in limiting its distribution. New Jersey was selected because a large amount of information is available from the publications of Smith (1950, 1952, 1953a, 1953b, 1957). The freshwater fish fauna of New Jersey may be divided into three groups: (1) species limited to the sluggish, brown-stained, acid lowland ponds and streams; (2) species of upland, clear, alkaline bodies of water; and (3) species



ure 8. The distribution of *Etheostoma fusiforme* in relation to the Fall Line. (Based on specimens examined)

found throughout the state in both types of situation. *Etheostoma f. fusiforme* belongs to the acid-water fauna (see species associates) which also includes *Enneacanthus obesus, Acantharchus pomotis, Mesogonistius chaetodon, Ictalurus natalis,* and *Aphredoderus sayanus.* These fishes are found in waters with pH values of 3.7 to 7.6 and usually 4.1 to 5.0 (Smith, 1953b). The average altitudes at which these acid-water species are found in New Jersey are: 52, 51, 98, 54, 64, and 54 feet, respectively. A number of widespread New Jersey species may be found with the preceding six species. These, together with their mean altitudinal ranges and their mean pH values, where known, are: *Erimyzon oblongus* (306, 6.70), *Notemigonus crysoleucas* (352, 7.11), *Ictalurus nebulosus* (366, 7.12), *Noturus gyrinus* (271), *Esox niger* (287, 6.46), *Umbra pygmaea* (266, 5.62), *Anguilla rostrata* (246), *Micropterus s. salmoides* (329, 7.30), *Lepomis gibbosus* (350), *Perca flavescens* (351, 7.13).

Cooper (1939) first reported *E. f. fusiforme* from southeastern Maine in the Ogunquit and Cape Neddick rivers, where I have also taken them. Subsequent collections in more northern parts of the state have not shown it to be present. Gordon (1937) and Bailey (1938) reported it in New Hampshire from the North and Isinglass rivers of the Coastal watershed and the Merrimack River. Hubbs and Cannon reported *f. fusiforme* from one pond on Cape Cod (as *fusiforme metae-gadi*). My collections made in the summers of 1956 and 1957 indicate that *E. f. fusiforme* is found in most of the ponds along the southern coast of Cape Cod but is absent in a number of ponds along the north shore. Hubbs and Cannon also were the first to report (1935) *E. f. fusiforme* from Gibbs Pond, Nantucket Island (as *fusiforme insulae*). They postulated the possible extinction of this form based on Cannon's unsuccessful attempt to collect additional specimens in 1933. I was able to collect eight specimens in a brief visit made in August 1956. Webster (1942) reported *E. f. fusiforme* from Pataganset Lake for the first Connecticut record, but did not find it in any other Connecticut ponds. I collected ten additional specimens from this lake in November 1957. Additional localities from the Thames drainage of Connecticut were reported by Behn and Wetzel (1960). Greeley (1939) w the first to record *E. f. fusiforme* from Lo Island, where the New York Biological S vey obtained it in Lake Ronkonkoma a in two tributaries of the Peconic Riv the Little River and Merritt Pond. Furth collecting over much of Long Island fr the summer of 1956 through 1959 has vealed moderately large *E. f. fusiforme* pop lations in Lower Lake Yaphank on the C mans River as well as in Lake Ronkonkor Two specimens were also taken in the o et stream of Wildwood Lake in the Peco River system. Its presence in the Maryla portion of the Delmarva Peninsula w shown by Mansueti (1951) and Mansu and Elser (1953). My collections exte the known range south to about six mi north of the Virginia-Maryland bord Hubbs and Cannon (1935) described *fu forme atraquae* from a Maryland collecti from the Potomac River and reported no s cess in collecting *f. fusiforme* in the a between the Potomac and Neuse riv Raney (1950) reported it from the Jan River where it has been taken well ab the Fall Line (Fig. 8). Since then a numb of additional specimens have been collec from the James, Nansemond, Chowan, a Roanoke rivers, thus filling in the distri tional gap. Frey (1951) and Frey a Bailey (1951) reported *E. f. fusiforme thermophilum* and *thermophilum oligo rum*) from the Bay Lakes of North Ca lina (except Black Lake).

Specimens Examined—Complete loca data are given for only those collecti which show range extensions or other s nificant distributional data. Other col tions are listed by drainage, state, cou and museum number. Complete data on most all of the collections may be found Collette (1960). A total of 3601 specim from 209 collections was examined.

Ogunquit Dr., Me.—York Co.: UMMZ 129 (12, 28-32); Ogunquit R., July 17, 1937. 31250 (7, 21-32); Ogunquit R. on US 1 in Og quit, Sept. 18, 1957.

Cape Neddick Dr., Me.—York Co.: UM 129639 (1, 34); Cape Neddick R., July 17, 1 CU 31245 (26, 22-36); Cape Neddick R. on 1, Sept. 18, 1957.

North-Isinglass Dr., 3 specimens, N.H.—R ingham Co.: UMMZ 163199. Strafford UMMZ 163198.

Merrimack Dr., 99 specimens, N.H.—Hills Co.: UMMZ 140883, 141243, 141244, 141 163218. Rockingham Co.: UMMZ 141 141246, 141247. Mass.—Essex Co.: CU 30 30428. Middlesex Co.: CU 30444; BU uncat.

swich Dr., 34 specimens, Mass.—Essex Co.: 15459, 30438.
assachusetts Bay Dr., 59 specimens. Mass.—dlesex Co.: USNM 1188 (1, 33) lectotype, M 94686 (25, 23-36), UMMZ 86582 (1, 38), MCZ 24589 (4, 27-36), paratypes of *Boleo-s fusiforme*; trib. of Charles R. at Framing-CU 30440; BU uncat.
eponset Dr., 22 specimens. Mass.—Norfolk CU 30533.
orth Dr., 9 specimens. Mass.—Norfolk Co.: 30464.
ape Cod, 386 specimens. Mass.— Barnstable USNM 77860 (1, 33) holotype and USNM 3 (36, 27-43) paratypes of *Hololepis fusi-is metae-gadi*; Temples Pd., Osterville; Nov. 902. CU 30475, 31602, 30487, 30490, 30503, 2, 31173, 31254, 31165, 30494.
ills River, 85 specimens. Cape Cod, Mass.—nstable Co.: 0.1 mi. W of jct. of Mass. 28 149 on Mass. 28. CU 30481, 31162, 31176, 1, 31170, 31538.
antucket Island, Mass.—Nantucket Co.: Gibbs MCZ 28274 (1, 24) holotype, MCZ 33547 16-27), UMMZ 86601 (2, 22-25) paratypes of *olepis fusiformis insulae*; Aug. 10, 1893. CU 2 (8, 21-30).
uzzards Bay Dr., 21 specimens. Mass. — nouth Co.: CU 30517.
aunton Dr., 35 specimens. Mass.—Bristol Co.: 30448. Bristol-Norfolk cos.: CU 20582. Ply-th Co.: CU 30768, 30769.
lackstone-Seekonk Dr., 27 specimens. Mass.—cester Co.: CU 30457.
ataganset Lake, 13 specimens. Conn.—New don Co.: CU 10182; UMMZ 138515; CU 06.
hames Dr., 31 specimens. Conn.—New Lon-Co.: UCF 136-9, 260. New London-Windham : UCF 140-5, 260.
ong Island, N.Y.—Suffolk Co.
ake Ronkonkoma, 114 specimens. NYSM 2441; 6527, 29993, 30265, 30279, 30347, 30529, 49.
ake Yaphank, 197 specimens: CU 30285, 30352, 05, 31850, 31133, 31847, 32697, 33194, 34098.
econic River, 3 specimens: NYSM 1452, 2410; 30258.
aritan Bay Dr., 56 specimens. N.J.—Middle-Co.: CU 30363. Monmouth Co.: CU 30371.
tlantic Coast of N.J. Dr., 484 specimens. ntic Co.: USNM 45142; CU 30390, 30398, 87, 31791, 31797, 32725, 32731, 32739. lington Co.: ANSP 20714, 31123; CU 13, 30382, 30389, 31803, 31794, 31781, 44. Cape May Co.: USNM 1338; ANSP 02-8. Ocean Co.: ANSP 55989; CU 27331, 71, 13163, 30374, 30380, 30381; UMMZ 413.
elaware Dr., 111 specimens. N.J.—Burlington ANSP 32571-2, 78737; CU 30416. Camden USNM 49085. Mercer Co.: ANSP 32598, 71-701, 40711-27. Pa.—Bucks Co.: Bristol. SP 32557-70, 32573, 40670.
tlantic Coast of Delmarva Peninsula, 90 speci-s. Del.—Kent Co.: ANSP 40728-31; CU 32083. sex Co.: CU 30606, 31172, 31168, 31171, 18, 34719. Md.—Worcester Co.: USNM 22.
hesapeake Bay Dr., 92 specimens. Del.—Sussex ANSP 40668-9; CU 31169. Md.—Caroline CU 18621, 18375; uncat. Worcester Co.: 33927, CU 33097, trib. of Pocomoke R., 10.8 S of Snow Hill.
otomac Dr., 41 specimens. Md.—Charles Co.: NM 100244, 103862, UMMZ 100677, 136032. ries-Prince Georges Cos.: Mattawoman Cr.: 21, 1933. UMMZ 107090 (1, 31) holotype; MZ 107089 (15, 28-32), USNM 117547 (2, 31), USNM 92946 (4, 32-34) paratypes of *olepis fusiformis atraquae*.
ames Dr., 15 specimens. Va.—Goochland Co.: NM 107470; UR 136, 262, uncat. Prince Ed-d Co.: USNM 197197.
ismal Swamp-Nansemond Dr., 15 specimens. —Norfolk Co.: USNM 100307, 100726; CU 51, 30253, 30255, 24625.
NM 107197.
howan Dr., 134 specimens. Va.—Dinwiddie : CU 30252. Greensville Co.: CU 30254. Sussex : CU 16880, 32090. N.C.—Gates Co.: UMMZ 483; CU 30143.

Roanoke Dr., 99 specimens. Va.—Greensville Co.: USNM 107554. N.C.—Bertie Co.: CU 29978. Halifax Co.: CU 29977. Martin Co.: CU 29980. Northhampton Co.: CU 17018, 31640.

Trent-Neuse Dr., 232 specimens. N.C.—Craven Co.: UMMZ 138484. Jones Co.: CU 30554. Johnston Co.: USNM 179731. Wilson Co.: USNM 179733.

Ellis Lake, 62 specimens. N.C.—Craven Co.: UMMZ 161986; CU 29983, 29985.

Cape Fear Dr., N.C.

Jones Lake, 193 specimens. Bladen Co.: DU uncat.; UMMZ 161968; CU 25304, 33107, 33715; UMMZ 161969 (1, 26) holotype of *Hololepis thermophilis oligoporus*.

Singletary Lake, 95 specimens. Bladen Co.: UMMZ 158771, 161965; CU 35131, 31951, 33720.

Salters Lake, 108 specimens. Bladen Co.: UMMZ 161973, 161975, 161974; CU 33108, 33707, 15562.

White Lake, 455 specimens. Bladen Co.: CU 25086, 15646, 33109, 31820, 33106, 34748; DU uncat.

Other Cape Fear Dr., 31 specimens. Bladen Co.: CU 33182. New Hanover Co.: Wilmington. USNM 52066, 52071, 86165, 86160, paratypes of *Hololepis thermophilus*. USNM 94687, 49144, 102149. Pender Co.: CU 29987, 33181. Harnett Co.: UMMZ 107072 (1, 33); Kipling, holotype of *Hololepis thermophilus*.

Waccamaw Dr., 92 specimens. N.C.—Brunswick Co.: CU 14257. Columbus Co.: UMMZ 161979, 161980, 161981, 161982, 161983; DU uncat; CU 31023, 14302, 31938, 34370.

Etheostoma fusiforme barratti (Holbrook)

Boleosoma Barratti—Holbrook, 1855:56-57 (original description).

Hololepis barratti—Putnam, 1863:4 (original description of *Hololepis* by Agassiz); Cope; 1864:233 (diagnosis of the species of *Hololepis*); Hubbs and Greene, 1928: 384-385 (*Hololepis* must replace *Copelandellus* confirmed by examination of Agassiz's specimens of *Hololepis "barratti"*); Hubbs and Cannon, 1935:54-62, pl. I, III, (description, range, synonymy); Carr, 1937: 84 (Fla.); Baker, 1939a:36-37 and 1939b: 45 (Reelfoot Lake, Tenn.); Kuhne, 1939: 93; Fowler, 1941:244, fig. 3, not 13 as given, (Suwannee R., Dixie Co., Fla.); Harkness, Pierce, and Lowe, 1941:112 (ecology, Lake Mize, Fla.); Driver, 1942:285 (in key, in part); Meehean, 1942:185 (lakes in Ocala National Forest, Fla.); Goin, 1943: 146 (water hyacinth community, Gainesville, Fla.); Fowler, 1945:40 (distribution table, Pee Dee, Santee, Savannah, Altamaha, St. Johns, Suwannee rivers), 195-196 (synonymy, S. C. records), 252 (Ga. records), 364 (Biloxi, Miss.); McLane, 1948:116-117 (in stomach of young *Micropterus salmoides* from St. Johns R., Fla.); Bailey and Hubbs, 1949:34 (characteristic Floridian species); Dickinson, 1949:26 (two shallow ponds near Gainesville, Fla.); Driver, 1950:298 (in key); McLane, 1950:196-199

(in stomach of rotenoned *Micropterus salmoides,* stomach contents of the *Hololepis,* Buck Pd., Fla.); Reid, 1950:179 (Orange Lake, Fla.); Freeman, 1952a:37 (Congaree R., S. C.); Freeman, 1952b:269 (Barnwell Co., S. C.); Reid, 1952:65 (around floating islands, Orange Lake, Fla.); Freeman and Huish, 1953:39, 44, 91-94, 96-102 (in stomachs of *Micropterus salmoides, Pomoxis nigromaculatus, Lepisosteus osseus, L. productus*); Anderson and Freeman, 1957:106 (Calhoun, Lexington, and Richland cos., Congaree R., S. C.); Randall, 1958:342 (Coastal Plain, Catawba-Wateree R., S. C.).

Poecilichthys quiescens—Jordan, 1884: 478-479 (original description).

Etheostoma quiescens—Woolman, 1892: 294, 297, 299, 300, 302 (description, habitat, Peace R., Hillsboro R., Withlacoochee R., Fla.).

Boleichthys fusiformis—Fowler, 1935:6, 23 (Santee, Cambahee, Edisto, Pee Dee r., Coastal Plain, S. C., in part).

Boleichthys barratti—Schrenkeisen, 1938: 235.

Hololepis barratti barratti—Bailey, 1950: 311-316 (comparison with *H. barratti appalachia*).

Hololepis barratti appalachia—Bailey, 1950:311-316 (original description).

Etheostoma barratti—Hubbs, 1952:486 (Caddo Lake, Texas); Moore, 1952:11 (Okla.); Bick, Hornuff, and Lambremont, 1953:230 (St. Tammany Par., La., misspelled *barrati*); Knapp, 1953:128 (range, in part), 126 (key to Texas fishes), fig. 167; Jurgens and Hubbs, 1953:4 (list of Tex. fishes); Bailey, Winn and Smith, 1954:144-145, 161 (Escambia R., Fla. and Ala.); Freeman, 1954:144, 146, 148, 154 (Salkahatchie and Savannah rivers, S. C.); Bailey and Gosline, 1955:20, 44 (number of vertebrae); Carr and Goin, 1955:31, 102 (description, habitat) pl. 30; Eddy, 1957: 220, fig. 547 (range, in part); Hubbs, 1957a:9 (list of Tex. fishes); Hubbs, 1957b:94 (distribution in Tex.); Moore, 1957:198; Briggs, 1958:275 (Fla.); Crittenden, 1958:217 (Bay Co., Fla.); Hubbs, 1958:11 (list of Tex. fishes); Cook, 1959: 35, 200, 203 (Miss.); Patrick, 1961: 257 (Savannah R.).

Etheostoma barratti appalachia—Bailey, Winn and Smith, 1954:144 (two introduced centrarchids in the pond from wh *E. b. appalachia* was taken).

Etheostoma fusiforme barratti—Colle 1961:2051.

Misidentifications—E. fusiforme barr as *Hololepis serrifer*—Fowler, 1945:2 (Savannah R., Ga., specimens re-examine as *Villora edwini*—Fowler, 1945:251-2 (two series from Piney Woods Lake, W Co., Ga., one series re-examined), 293-2 (seven series from Florida, five of wh were re-examined).

Types—MCZ 24571 (5 specimens, 37 45.8 mm), from "Florida." The holot of *Poecilichthys quiescens* is USNM 255 a 35.5 mm male from a tributary of Suwanee R. near Nashville, Georgia.

Diagnosis—Distinguished from the ot species of the subgenus *Hololepis* by a co bination of the following characters: t anal spines; interorbital pores absent; p operculomandibular pores usually nine; fraorbital canal incomplete; breast co pletely scaled. Distinguished from *E. fo forme fusiforme* by the following: p opercle more often partially serrate (36 of specimens examined); infraorbital po usually 1 + 3 (70%); more interorbi scales (1-37, $\bar{x}$: 13.2); parietal more co pletely scaled (usually over 25%, $\bar{x}$: 5%). Maximum size of males 46.2 m (USNM 99988, Hillsborough Co., Fla.) a of females 46.6 mm (CU 35102, San River).

Coloration—The range of variation generally similar to that of *E. f. fusiform* both forms are extremely variable.

In both sexes there is a tendency tow the development at the base of the cau of a supramedian spot in addition to t submedian spot present in *E. f. fusifor* When present, the supramedian spot is as intense as the submedian. The tender toward the formation of a median band the first dorsal fin occurs more often populations of *f. barratti* than in *f. fo forme*. This tendency was also noted in second dorsal and anal fins in some spe mens. A male from the Okefenokee Swa showed the most extreme development pigmentation (Fig. 10) of any *fusifor* males that were examined. The patterns breeding males and females from four calities are shown (Figs. 9 and 10).

As noted by Collette and Yerger (196

ure 9. Breeding patterns of female *Etheostoma fusiforme barratti.* (from top to tom) CU 29752; 40.2 mm; Ga., Bullock Co., Ogeechee dr.; Feb. 15, 1951. UG 201; 3 mm; Ga., Charlton Co., Okefenokee Swamp; Apr. 10, 1951. UG 205; 24.5 mm; , Irwin Co., Crystal Lake; May 5, 1951. DU uncat; 32.8 mm; N.C., Henderson Co., nch Broad dr., date unknown but apparently past height of breeding season. (Photo-ph by Douglass M. Payne)

drawing in Fowler (1941: Fig. 13) eled as *Hololepis barratti* is reversed with one labeled as *Villora edwini* (Fig. 3).

Genital Papilla—The genital papilla of breeding female is like that in *E. fusi-me fusiforme* (Fig. 1f) and *E. gracile* g. 1c).

Breeding Tubercles—Tubercles are pres- on the anal and pelvic fin rays as in *fusiforme fusiforme,* but are frequently present on the pelvic and second anal nes. Besides showing a greater develop-nt of breeding tubercles than in *E. f. fusi-me*, the tubercles are present for a longer iod of time. In the Ochlockonee popula-tion, tubercles have been found on speci-mens taken from December 17 through April 13. Tubercles have been found as early as October 27 (Suwannee to Ochlock-onee population, FSU 3273) and as late as May 29 (UG 516, Pee Dee population). In these collections not all males have tu-bercles, and some specimens have them only on the pelvic fins. Specimens with tuber-cles on both anal and pelvic fins were taken in the period from March 25 to May 29. The spawning period varies between popu-lations but should be within the period that tubercles are developed to their maximum extent.

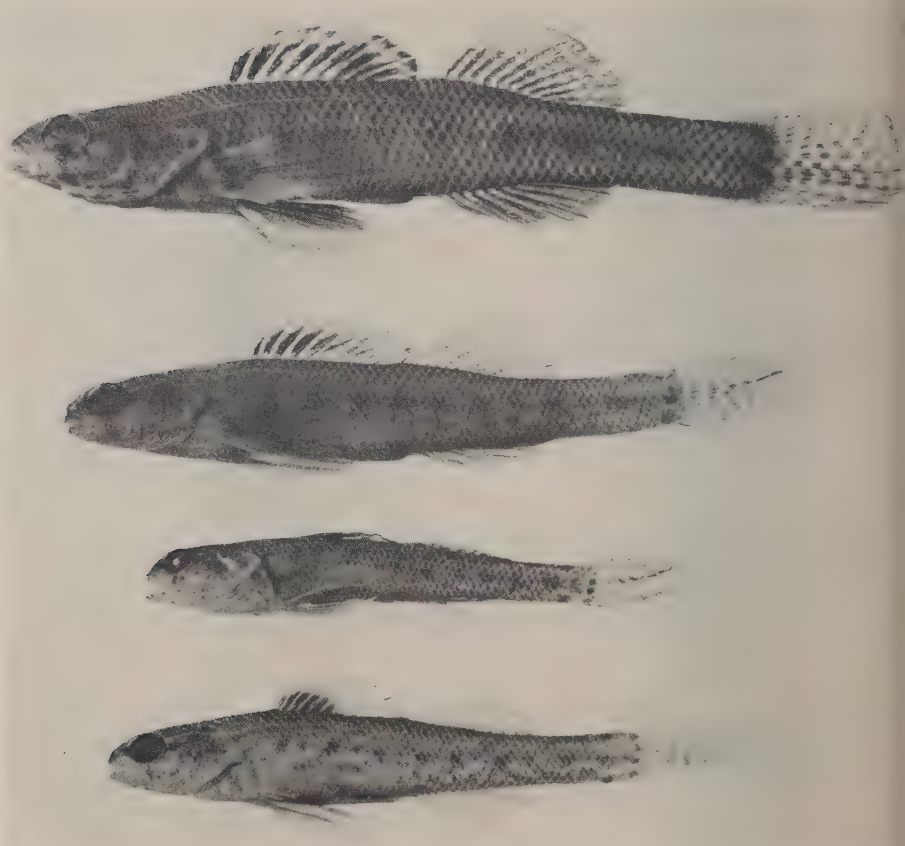


Figure 10. Breeding patterns of male *Etheostoma fusiforme barratti.* (from top to bo tom) UG 201; 46.7 mm; Ga., Charlton Co., Okefenokee Swamp; Apr. 10, 1951. TU 793 37.8 mm; Miss., Pearl River Co., Pearl dr.; Mar. 21, 1952. UG 205; 28.1 mm; Ga., Irw Co., Crystal Lake; May 5, 1951. DU uncat; 32.5 mm; N.C., Henderson Co., Fren Broad dr., date unknown but apparently past height of breeding season. (Photograp by Douglass M. Payne)

The distribution of breeding tubercles on the pelvic fins of male *E. f. barratti* is essentially the same as in *E. gracile* (Fig. 1k). The distribution on the anal fin of a male *f. fusiforme* (Fig. 1j) is similar to the distribution in *f. barratti,* except that in the latter the tubercles are more likely to be on the second anal spine.

Development—As in *E. fusiforme fusiforme,* both the supratemporal canal and the number of pored lateral-line scales change with age. The supratemorpal canal is incomplete in young specimens (16.8 to 20.1 mm) from Crystal Lake, Georgia (UG 205) (Table 31); the transition period e tends from 20.5 mm to 22.0 mm; and t supratemporal canal is complete in spec mens 22.0 mm and larger. In specime from the Arlington River, Florida (U 6945), the juvenile period extends to 21 mm, the transition period from 21.5 27.4 mm, and the supratemporal canal complete in specimens larger than 27.4 m (Table 31). In a series of collections fro Lake Fairview, Florida (ANSP) the juv nile period extends to 19.9 mm and t transition period is completed by 24.9 m (Table 31).

12.6 mm specimen from the Okeechodrainage (CU 35069) has scales on the lal peduncle and extending forward g the lateral line to a point opposite the base of the first dorsal fin. A 16.8 mm imen in this collection has the body rmation nearly complete but has only pored lateral-line scales; a 21.6 mm imen has 11 pored scales, and the other specimens (22.8 to 27.2 mm) have 15-pored lateral-line scales. The incomplete elopment of pored lateral-line scales in ts from Crystal Lake, Georgia, will be ussed under geographic variation, pored ral-line scales.

labitat—Basically the habitat of *E. fusine barratti* is the same as that of the ninate form: swamps, backwaters of ams, sloughs and lakes. Goin (1943) d *E. f. barratti* as part of the lower verate fauna associated with water hyahs (*Eichornia crassipes*) around Gainese, Florida. In Orange Lake, Florida, Reid 50 and 1952) found *E. f. barratti* both hallow shore zones and around the edges floating islands composed of arrowhead *gittaria*) and pickerel weed (*Pontederia*) e distance from shore. The characters Florida stream containing *E. f. barratti* contrasted with those of a stream coning *Etheostoma* (*Villora*) *edwini* under account of the latter species in Collette Yerger (1962).

pecies Associates—J. R. Bailey (1950) d *Chaenobryttus gulosus, Lepomis m. hrochirus,* and *Lepomis auritus* as assoes of his *Hololepis barratti appalachia.* M. Bailey, Winn, and Smith (1954) d the presence of *Chaenobryttus* and *L. itus* at the type locality of *E. b. appaia* as an indication that it is merely the duct of an introduction.

Woolman (1892), in reporting on the es of central Florida, found *E. f. barratti* leven localities. Species commonly found him with *f. barratti* and the number of es taken were: *Gambusia affinis* (11); *enobryttus gulosus* (11); *Fundulus ysotus* (8); *Jordanella floridae* (7); *omis machrochirus* (7); and *Elassoma rgladei* (7).

Predators—From lakes Eustis and Harris, rida, Freeman and Huish (1953) reed *E. f. barratti* from the stomachs of *cropterus salmoides, Pomoxis nigromaculatus, Lepisosteus osseus,* and *L. productus.* McLane (1948) reported one *E. f. barratti* from the stomach of a young (47-229 mm) *Micropterus salmoides floridanus* from the St. Johns River. After rotenoning, McLane (1950) also reported 500 *E. f. barratti* from 62 *M. salmoides floridanus* stomachs from Buck Pond, Marion County. One had eaten 47 *f. barratti.* He noted that most of the bass may have taken *f. barratti* during the poisoning operation. It seems likely that any larger fish will feed on *E. f. barratti* if they are available.

Habits—McLane (1950) found 82 *Chaeborus,* 37 *Chydoras,* 15 *Cyclops,* 2 Chironomidae, and 2 Amphipoda in nine stomachs of *E. f. barratti* from Buck Pond, Florida.

Distribution—Found from the Pee Dee River of North and South Carolina south along the Atlantic Coastal Plain below the Fall Line throughout most of peninsular Florida; west along the Gulf Coastal Plain as far as Caddo Lake on the Texas-Louisiana border; and north in the former Mississippi Embayment as far as McCurtain Co., Oklahoma and Reelfoot Lake, Tennessee (Fig. 8). Also known from a few ponds in the vicinity of Asheville, North Carolina, in the French Broad River system, but this population is believed (Bailey, Winn, and Smith, 1954) to be the result of an introduction.

Hubbs and Cannon (1935: pl. III) gave the range of *E. f. barratti* as the Pee Dee River south to the Peace River of Florida and west as far as the Suwannee River drainage of Georgia and Florida. Since then Baker (1939a) reported one specimen from Reelfoot Lake to which I have added another specimen from a collection made in June, 1959. Although Cook (1959) stated that there were no positive records from Mississippi, it has been taken at a number of localities in that state as indicated under the specimens examined.

The presence of *E. f. barratti* in southeastern McCurtain County, Oklahoma, reflects the influence of the Coastal Plain on the fish fauna of this region, as noted by Reeves and Moore (1951) for *Lepomis marginatus, L. symmetricus, Fundulus notti dispar, Centrarchus macropterus,* and *Elassoma zonatum.*

Etheostoma f. barratti has been taken from several other localities in the Red River

system: Caddo Lake on the Texas-Louisiana border (Hubbs, 1952) and from various localities in the northern part of Louisiana. Hubbs (1957b) listed several species that occur in the Red River system east of Lake Texoma but are absent from the Sabine and other drainages to the west such as: *Esox niger, Moxostoma erythrurum, Notropis cornutus, N. ortenburgeri, Menidia audens, Stizostedion canadense* and *E. f. barratti.*

A specimen with the locality data of "Spring Creek, Texas," (USNM 118555) must come from west of Caddo Lake and so is the western-most record of *E. f. barratti,* but due to the large number of places with this name in Texas, the exact locality is unknown.

As Briggs (1958) pointed out, only one of the 11 Florida percid fishes (*E. f. barratti)* is found in the southern part of the peninsula. He gave the distribution of *E. f. barratti* as south to Lake Okeechobee. Woolman (1892) reported *f. barratti* as far south as the Peace River on the Gulf Coast. Recent collections have extended the range farther south into Collier Co. on the west coast (TU 20719) and into Dade Co. near Miami on the east coast (USNM 195862).

Figure 8 shows how clearly the Fall Line delimits the range of *E. f. barratti,* particularly in the Congaree watershed of South Carolina, where a large number of collections show *E. f. barratti* (and *E. serriferum,* Fig. 3) below the Fall Line and *E. saludae* above it (Fig. 3). It is also of interest to compare Fig. 5 of the distribution of *E. gracile* with Fig. 8. This comparison will show that although there is a large overlap in the total ranges of *E. gracile* and *E. f. barratti,* there are relatively few localities where both have been taken together (Reelfoot Lake, Tenn.; Caddo Lake, Tex.; SE McCurtain Co., Okla.; Ouachita Parish, La.).

Specimens Examined—Complete locality data are given only for those collections which show range extensions or other significant distributional information. Other collections are listed by drainage, state, county, and museum number with the total number examined for each drainage. Complete data for most of the collections can be found in Collette (1960). A total of 2265 specimens from 339 collections was examined.

Pee Dee Dr., 49 specimens. N. C.—Richm
Co.: CU 19570; UG 516. Scotland Co.: UG
S. C.—Florence Co.: CU 19189. Georgetown
ANSP 61023-6. Lee Co.: CU 28217.

Santee Dr., 78 specimens. S. C.—Berkeley
USNM 116236. Clarendon Co.: CU 26250.
shaw Co.: CU 35104, 35121, 35123, 35110, 351
USNM 195865, 195866. Lexington Co.: CU 35
35122, 35116. Lexington-Calhoun cos.: CU 35
Richland Co.: CU 35117, 35125, 35112, 35
35113, 35127, 35115, 35105, 35129, 35103, 351
USNM 149254. Sumter Co.: CU 35132.

Charleston Harbor Dr., 13 specimens. S.
Charleston Co.: USNM 1143 and 1161. Dorche
Co.: USNM 1185.

Edisto Dr., 16 specimens. S. C.—Bamburg
CU 35114, 35101. Colleton Co.: ANSP 54
Orangeburg Co.: CU 19080, 30622.

Combahee-Broad Dr., 14 specimens. S.
Barnwell Co.: CU 35118, 35109, 35128. Jas
Co.: CU 32662.

Savannah Dr., 336 specimens. S. C.—Aiken
ANSP 73458; UG 247, 270; CU 35107, 35
24325, 30882; ANSP 78845, 78494; USNM 195
Allendale Co.: ANSP 73409, 74263, 78875;
252; UMMZ 167889; CU 30897; USNM 162
162531, 162532. Barnwell Co.: CU 35120, 35
35111, 24396; ANSP 78899, 80401; US
195863. Jasper Co.: UMMZ 155201. Ga.—Ch
ham Co.: ANSP 79858. Richmond Co.: UM
158026; CU 17628, 17209; UG 177; US
86194, 82624, 82625.

Ogeechee Dr., 49 specimens, Ga.—Candler
UG 152, 152B. Bryan Co.: CU 30322; TU 164
Bullock Co.: CU 30627, 30625, 30626, 306
30624, 29752, 29762. Jenkins Co.: USNM 434
61567.

Altamaha-Satilla Dr., 54 specimens. Ga.
Appling Co.: CU 29756. Brantley Co.: UG 4
TU 21200. Coffee Co.: BU uncat. Dodge
CU 17702. Emmanuel Co.: UMMZ 158045;
17686. Irwin Co.: CU 29748; UG 292, 29
Jeff Davis-Montgomery cos.: UG 259. John
Co.: TU 14298. Tattnall Co.: CU 29755. Toom
Co.: UMMZ 158062. Washington Co.: CU 297

St. Marys Dr., 69 specimens. Ga.—Cam
Co.: ANSP uncat. Charlton Co.: CU 516, 5
522, 4043, 35136, 35137, 35135; UG 200;
21309. Fla.—Baker Co.: CU 12615, 21088;
21212.

St. Johns Dr., 188 specimens. Fla.—Brev
Co.: UMMZ 158576. Duval Co.: UF 6945. Fl
ler Co.: USNM 125479, 170976. Lake Co.:
12519; CU 35140. Seminole Co.: ANSP unc
CU 24572. Volusia Co.: UF 6940; USNM 1332

Indian River Dr., 1 specimen. Fla.—Brev
Co.; USNM 25343.

St. Cloud, Fla.—Osceola Co.: UMMZ 158
(39, 24-38); canal between Alligator and Li
Lakes near St. Cloud; Dec. 28, 1939.

Orlando isolates, 204 specimens. Fla.—Ora
Co.: USNM 44413, 106941, 133527, 1335
133509, 133517, 133516; ANSP 4 uncat. col

Oklawaha-St. Johns isolates, 90 specimens.
—Clay Co.: CU 35067. Marion Co.: UMMZ 1106
158125, 166544, 166601; UF 6958; CU 262
Osceola Co.: UMMZ 158606. Putnam Co.:
35068.

Lake Okeechobee Dr., 47 specimens. Fla.
Hendry Co.: CU 35069. Highlands Co.: O
uncat.; CU 24236. Indian River Co.: UF 69
Osceola Co.: CU 8614, 10235, 12030, 239
UMMZ 158555; FSU 2496.

Dade Co., Fla.—USNM 195862 (1, 19);
suburbs of Miami, canal near Milam Dairy
and Ludlum Rd.; Apr. 7, 1960.

South Florida isolate—Collier Co.; TU 20
(54, 18-38); canal 11.2 mi. E. jct. US 41
Fla 846, or 21.6 mi. NE of Naples; July
1959.

Charlotte Harbor Dr., Fla.—Charlotte C
UMML 4754 (3, 33-39); roadside canal 8.5
E of Punta Gorda on Fla. 74; Dec. 22, 1957.

Tampa Bay Dr., 46 specimens. Fla.—Hi
borough Co.: UMMZ 139251; CU 12731, 211
TU 208, 3054, 3772, 4626; FSU 1846; US
100029, 100050; 99988, 170974, 99956, 1069
Pasco Co.: TU 20737. Pinelas Co.: CU 122
Polk Co.: CU 26256.

Withlacoochee-Waccasassa Dr., 101 specime
Fla.—Citrus Co.: TU 9842. Citrus-Marion
FSU 2131. Lake-Polk cos.: CU 35139. Levy C

2796, 24550; UF 2903; TU 15672; USNM
2, 106939.
wnan Lake Dr., 84 specimens. Fla.—Alachua
UF 6944; UG 9; CU 12302, 12846, 16035;
M 88490, 93715.
wannee Dr., 68 specimens. Ga.—Berrien
USNM 28509 (1, 37); trib. of Alapaha R. at
ville; holotype of *Poecilichthys quiescens*.
Co.: CU 29601; UG 208. Lanier Co.: USNM
; BU uncat. Lowndes Co.: UG 458. Wilcox
CU 17652, 17411. Fla—Bradford Co.: USNM
). Columbia Co.: CU 12500; UF 8301. Dixie
ANSP 69213. Hamilton Co.: UMMZ 163310;
4465. Lafayette Co.: UMMZ 166609.
rstal Lake, Ga.—Irwin Co.: UG 205 (26,
); Crystal L., 4.5 mi. N Irwinville; May 5,

efenokee Swamp, 88 specimens. Ga.—un-
n co.: ANSP 55935; USNM 153440. Charl-
Co.: CU 8610-3, 257-60, 353-4, 262-5, 129,
340, 535, 6-7 9-10, 325; ANSP 79923; UG
USNM 153433. Ware Co.: ANSP 70564;
7322; UMMZ 138720.
nholloway to St. Marks Dr., 30 specimens.
-Lafayette Co.: CU 12202. Leon Co.: FSU
; TU 9763. Madison Co.: CU 12484. Taylor
TU 5056. Wakulla Co.: UMMZ 163428;
887.
hlockonee-New Dr., 122 specimens. Ga.—
itt Co.: CU 17504. Grady Co.: UG 102,
FSU 2887. Thomas Co.: FSU 3970. Fla.—
den Co.: UF 6956, 4889; FSU 306, 2167,
; TU 22590. Leon Co.: FSU 400, 67, 74,
1300, 3609, 2091. Liberty Co.: UMMZ
33; FSU 230, 2267, 3755; TU 1116.
alachicola Dr., 102 specimens. Ga.—Baker
UG 31, 27, 36. Crisp Co.: UG 6. Dougherty
UMMZ 164001, 164039; BU uncat. Early
UG 25A. Sumter Co.: UMMZ 163989. Taylor
CU 30319. Fla.—Franklin Co.: FSU 2767.
den Co.: UMMZ 166266. Gulf Co.: FSU
; TU 20540, 22453. Jackson Co.: FSU 2679,
2701, 2733.
octawhatchee to Perdido Bays, 64 specimens.
-Bay Co.: UMMZ 163450. Escambia Co.:
2916. Escambia-Santa Rosa cos.: ANSP
2, 73028, 79004; UMMZ 165074. Holmes
UMMZ 163501; TU 20406. Okaloosa Co.:
3694, uncat. Santa Rosa Co.: UMMZ 155507,
19; ANSP 73060; TU 10489. Walton Co.:
311, 20865, 22730, 22775, 23154.
known Fla. Dr., 48 specimens.—USNM
4, 92896, 106941.
obile Bay Dr., Ala.—Mobile Co.: TU 6257
0-41); Hall's Mill Cr. at Navco, trib. of Dog
Feb. 11-13, 1938. Washington Co.: UMMZ
99 (4, 33-38); Bilbo Cr., on US 43 near
tosh, T3N, R1E, Sec. 7; Apr. 12, 1941.
ssissippi Sound Dr., Miss.—Hancock Co.: TU
(6, 32-42); Bayou Phillip, trib. to Jordan R.,
ml. E of Waveland on rt. 90; Mar. 9, 1953.
ison Co.: ANSP 55746 (1, 36); 3 mi. N
loxi in cypress cr.; Mar. 15, 1932. Stone
USNM 195873 (1, 36); Red Cr. near US
ear Wiggins; May 13, 1933.
arl R.—Lake Pontchartrain Dr., 41 specimens.
—Pearl River Co.: Hobolochitto Cr., 0.9
N of Picayune on US 11: TU 7937, 14103,
7670, 16773; UMMZ 166128; CU 31890.
St. Tammany Par.: CU 32247 (1, 40); 8
W of Slidell. TU 379 (1, 34); slough at
d bridge W of Pearl R. on Hickory Rd.
755 (1, 38) and TU 835 (1, 35); Talisheek
0.3 mi. N of Talisheek. TU 8159 (1,40);
along W Pearl R., 13 mi. N of the town
earl River. TU 15144 (2, 34-37), TU 17369
34-40), and TU 17413 (4, 35-38); Talisheek
at Talisheek on La. 41. Tangipahoa Par.:
3574 (1, 40); Selser Cr., 3.3 mi. E of Ham-
l on rt. 7.
zoo Dr., Miss.—Warren Co.: USNM 129093
8); Yazoo R. at bridge on US 61 near Vicks-
; May 1933. Yazoo Co.: USNM 170977
6); Little and Big Kilby Lakes, Yazoo City;
2, 1933.
elfoot Lake, Tenn.—Obion Co.: UMMZ
97 (1, 39); stagnant basin at N end of
July 26, 1937. CU 33345 (1, 20); N
of lake by Oak Log Lodge near the Reelfoot
gical Station; June 27, 1959.
d River Dr., La.—Caddo Par.: USNM
36 (9, 21-26); Black Bayou L., 0.5 mi. above
dam on E side of lake, sec. 23, T22N, R15W; July 24, 1956. Ouachita Par.: UMMZ uncat. (2, 30-40); Cheniere Cr. below dam of Cheniere L., Sec. 17 and 20, T17N, R3E; June 6, 1956. Union Par.: USNM 172708 (8, 21-27); Bayou de l'Outre at La. 2, Hattick Lake, sec. 20, T20N, R3E; June 18, 1955. Okla.—McCurtain Co.: OAM 3078 (8, 25-31); Aug. 20, 1948; and CU 33747 (8, 20-25); June 24, 1959; cypress swamp 3 mi. S of Eagletown on dirt road. Tex.—Harrison Co.: OAM 4732 (9, 29-39); 3.5 mi. NE of Kernack on Caddo Lake; Mar. 24, 1951.

Unknown Texas Dr.—USNM 118555 (1, 36); Spring Cr.; Apr. 23, 1940.

French Broad Dr., N. C.—Buncombe Co.: pond S of mouth of Bent Cr., 300 ft. W of the French Broad R., 7 mi. SSW of Asheville. UMMZ 156224 (1, 37) holotype, UMMZ 156225 (49, 17-43) paratypes, July 14, 1947, and CU 18444 (3, 30-40), June 7, 1949, paratypes of *Hololepis barrati appalachia*. Henderson Co.: DU uncat. (12, 28-38); Cane Cr. oxbow, 1 mi. SW of Fletcher, 1 mi. above mouth of Cane Cr. into French Broad R.; 1952.

1. *Geographic Variation in Etheostoma fusiforme*

Variation in the characters examined for the two valid subspecies (*E. fusiforme fusiforme* and *E. fusiforme barratti*) will be discussed in this section (Tables 18-31). Nine names presently apply to segments of this species. From north to south they are: *fusiforme fusiforme* (Girard) from southern Maine through Massachusetts, exclusive of Cape Cod; *f. metaegadi* (Hubbs and Cannon) from Cape Cod; *f. insulae* (Hubbs and Cannon) from Nantucket Island; *f. erochroum* (Cope) from New Jersey and the Delmarva peninsula; *f. atraquae* (Hubbs and Cannon) from the Potomac River; *thermophilum thermophilum* (Hubbs and Cannon) from the Neuse, Cape Fear, and Waccamaw rivers, and White Lake; *t. oligoporum* (Bailey and Frey) from the dark-stained North Carolina Bay Lakes (Salters, Jones, Singletary) in the Cape Fear drainage; *barratti barratti* (Holbrook) from the Pee Dee River south through most of penisular Florida, west to the Red River in Texas and Oklahoma, and north in the Mississippi Embayment as far as Reelfoot Lake, Tenn.; and *b. appalachia* (Bailey) from the French Broad River, near Asheville, N.C. The validity of these nominal forms will be discussed below.

Total Lateral-line scales (Table 18): Hubbs and Cannon (1935:83) gave the number of total lateral-line scales of their *Hololepis fusiformis insulae* from Nantucket as "somewhat fewer than in typical *fusiformis* and much fewer than in *metaegadi*." This was true on the basis of the one Cape Cod collection on which *metaegadi* was based and a few more recent

collections. However, at one Cape Cod locality, Mills River, counts are intermediate between *insulae* and *metaegadi* ($\bar{x}$: Nantucket-44.71, Mills River—48.84, and the rest of Cape Cod—52.34). There is also a reduced mean number of total lateral-line scales in some other scattered populations: the Weweantic River just to the west of Cape Cod ($\bar{x}$: 48.35); the coastal streams south of Raritan Bay, New Jersey (46.58); the James River of Virginia (46.57); and Crystal Lake, Georgia (46.04).

Several populations have more total lateral-line scales than *f. metaegadi:* Lake Ronkonkoma, N.Y. ($\bar{x}$:55.71); Pataganset Lake, Conn. (54.62); Lake Yaphank, N.Y. (54.13); Pearl-Pontchartrain, La. (55.10); Red River (55.68).

Pored lateral-line scales (Table 19): The major difficulty with regard to this character is the great amount of variation present (0-37 scales). This is particularly true in a number of natural lakes in North Carolina, known as the Bay Lakes.

Although the Carolina Bays have long been a subject of geological investigations to determine their mode of origin, relatively little is known about the biology of the few lakes that remain in the Bays. Fowler (1942) and Hubbs and Raney (1946) described four endemic species of fishes from Lake Waccamaw, the largest of the southern North Carolina natural lakes. Later (Frey, 1951), *Notropis waccamanus* Fowler was reduced to a synonym of *N. petersoni* Fowler. Frey (1948a, 1948b), Hueske (1948), and Louder (1958, 1959) published a series of popular papers about the lakes and their fauna.

Frey also published a series of scientific papers (1949, 1951) and Bailey and Frey (1951) recognized two subspecies of *Hololepis thermophilum* from the Bay Lakes. They named the form in the dark stained lakes *thermophilum oligoporum* and considered the nominate form to be present in the clearer lakes (White, Ellis, and Waccamaw) as well as in the Cape Fear and Neuse rivers. Bailey and Frey (1951) were aware of the biogeographic difficulties in this allocation of subspecies: lakes White, Waccamaw and Ellis each belong to a separate major Atlantic drainage while the dark lakes (Jones, Salters, Singletary) along with White, are found in the Cape Fear system. Bailey and Frey discussed the possibility of polyphyletic origin of *t. oli porum.* I believe that taxonomic recogni should be withheld when polyphyletic ori of a subspecies is suspected.

A special search was made for a reas able explanation for the presence of different forms in the dark and light Lakes. The explanations proposed based on an intensive study of the Lakes and their fishes. The best dif entiating character lies in the number pored lateral-line scales, which is consi ably reduced in the dark lakes. Frey (19 noted a similar situation, with the *P flavescens* and *Chaenobryttus gulosus* f the darker lakes having fewer total late line scales, but considered these to be c of ecotypic variation. Bailey and (1951) rejected the possibility that t *thermophilum oligoporum* was an ecot variation.

The correlation between water color number of lateral-line scales might be not to color *per se,* but to productiv Therefore, the productivities of the l were compared. Productivity is cha terized in many different ways so sev methods of estimation were utilized, b physical-chemical and biological.

Increased productivity is frequently related with increased carbonate cont Carlander (1955) showed a positive relation between fish crop and me orange alkalinity in trout lakes, warm ter lakes, and reservoirs. Moyle (19 showed a positive correlation between y of pikeperch and total alkalinity. (1949) presented a summary table physical and chemical characteristics of Bay Lakes. He gave the alkalinity in N/44 H_2SO_4 because there is some sulphuric acid present in some of the la Thus the alkalinity cannot be stated in usual manner (parts per million of me orange alkalinity). However, it is appa that the lakes fall into two catego (Table 28); a low alkalinity group, Bladen County Lakes (Black, Jones, Sal Singletary, White) and a high alkalinity (Waccamaw). This high alkalinity is parently due to the solution of lime other minerals from the outcrops of calcareous Duplin formation, and of older Cretaceous formation along the no east shore (Clark, *et al.,* 1922).

The pH of lakes is also correlated

ductivity. Smith (1952, 1953b) noted low productivity of New Jersey waters h a pH below 6.0. Renlund (1950) ed the absence of a number of plants pecially species of *Potamogeton*) from acid lakes of southern New Jersey. ble 28 shows the pH as taken from y (1949). Again there are two distinct ups; the Bladen County Lakes on the hand and the more alkaline Wacca- w on the other.

Shoreline development is also correlated h productivity (Welch, 1952) since in- ased irregularity of shoreline results in ater contact of water with land, in- ased area of protected bays, greater diver- cation of bottom and margin conditions, reased areas of shallow water for growth rooted vegetation, and increased op- rtunity for close super-position of the otosynthetic zone upon the decomposition ne. The last two factors are of no im- rtance here because all the lakes are so llow. These lakes are all oval with few egularities, so the figure for shore line velopment (Table 28) is quite close to the value for a perfect circle. Singletary ke has an artificial dredged channel, 160 rds long, in the outlet creek and so has highest value (1.17).

Another factor that limits productivity the amount of light energy that reaches phytoplankton; that reaching a certain pth in a lake is due to differences in trans- rency which in turn varies with three fac- rs: color of the water; amount of or- nic and inorganic material in the water; d the amount of plankton present (Rutt- r, 1953). The first two factors are of portance in the Bay Lakes. Frey (1951) ve the actual color of the water in parts r million of potassium chloroplatinate Table 28). However, the scattering of the diation by suspended materials is just important as the absorptive function of e coloring material in these lakes. Single- ry, Black, and Salters lakes have larger antities of non-living organic materials an do the other lakes. Light penetration, measured with the Secchi disc, takes into nsideration both of these factors. Based Frey's mean Secchi disc readings, the kes fall into three groups (Table 28): w light penetration (Black, Jones, Salters, ngletary); moderate penetration (Wac- maw); and high penetration (White).

Table 29 ranks the physical-chemical indices of productivity from 1 to 6 and the totals of these rankings give a physical-chemical index of productivity by means of which the lakes may be arranged in order of increasing productivity namely: Black, Jones, Salters, Singletary, White, Waccamaw.

Certain biological characteristics can be used to measure productivity. One of these is the relative amount of rooted aquatic vegetation. Data from Frey (1948a, 1948b, 1949), Louder (personal communication), and personal observation classify the lakes as follows: 1. no rooted aquatics (Black, Jones, Salters); 2. small amount, especially in the artificial channel (Singletary); 3. moderate amounts (White and Waccamaw). In addition to being a measure of productivity, the amount of aquatic plants present has a direct effect on productivity. One of the reasons that the darker lakes are so unproductive is that there are few aquatics present to provide food, cover, and spawning sites for fishes and other animals. The lack of abundant rooted aquatic vegetation is caused in part by the dark water which prevents photosynthesis at other than very shallow depths.

The number of species of fish (or other animals) present may also be used as an indication of relative productivity. Frey (1951) listed the species of fishes collected during the 1947 survey as follows: Black-8; Salters-11; Jones-12; Singletary-13; White-17; and Waccamaw-25. Since then my collections and those made by Darrell E. Louder (1959 and personal communication) have added to the number of species taken in all of the lakes (Table 30). Frey (1951) pointed out that there is a group of 11 species in almost all of the lakes (Table 30) with *Etheostoma f. fusiforme* and *Esox niger* lacking only in Black Lake. *Aphredoderus sayanus* may now be added to this list and is absent only from Jones Lake. In the various lakes, additional species are found correlated with increased productivity until Waccamaw is reached, which has all but one of the species present in the other lakes. Here *Fundulus notti lineolatus* is replaced by the endemic *F. waccamensis*. Frey noted that probably none of the species of *Lepomis* is native to the Bladen County lakes. Introductions have of course been attempted, from which subsequent re-

TABLE 31.

Development of the supratemporal canal in Etheostoma fusiforme

Size (mm)	*E. fusiforme fusiforme*												*E. fusiforme barratti*					
	Long Island		Jones L.		White L.		Singletary L.		L. Waccamaw		Salters L.		L. Fairview		Arlington R.		Crystal L.	
	com.	inc.	com.	inc.	com.	inc.	com.	inc.	com.	inc.	com.	inc.	com.	inc.	com.	inc.	com.	inc.
12.0-13.9		3		2				2										
14.0-15.9		8		6		17		9				3						3
16.0-17.9		8		4		30		6		1	1	14						2
18.0-19.9		9	3	15	6	29		17	3	10	7	17		7		2		2
20.0-21.9	3	14	3	4	21	16	1	11	8	12	6	14	3	8	1	3	3	1
22.0-23.9	12	9	16	5	35	16	3	3	5	3	4	14	3	5	8	5	5	1
24.0-25.9	18	5	10		32	7	2	8	13	—	1	4	4	1	13	3	6	
26.0-27.9	20	—	7		9	7	5	11	4	2		1	2		7	1	1	
28.0-29.9	19	1	1		2		4	7	1	—		—	2		3		1	
30.0-31.9	10	—	1		1		1		6	2		1	—		—			
32.0-33.9	24	—					—		4			1	1		2			
34.0-35.9	27	—					—											
36.0-37.9	36	2					—											
38.0-39.9	23	—					—											
40.0-41.9	10	1					1											
42.0-43.9	20																	
44.0-45.9	7																	
46.0-47.9	4																	
48.0-49.9	1																	
50.0-51.9																		

(The horizontal lines mark the extent of the transition period, with the juvenile condition above the top line and the adult condition below the bottom line. Inc. = incomplete, com. = complete.)

TABLE 32.

Number of pored lateral-line scales in Etheostoma collis and E. saludae

Form and drainage	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	$\bar{x}$
collis lepidinion																											
Roanoke						1	–	–	4	3	4	4	3*	6	1	1	1	1									16.17
Neuse								1	1	1	2	1															14.17
Cape Fear														1**													–
collis collis																											
Yadkin-Pee Dee					1	–	4	2	4	3	4	3	2	2	–	1	2	1	1	1							15.48
Rocky-Pee Dee						3	1	2	3	2	3	4	1	1	–	–	1	–	–	–	–	–	–	–	–	1	14.86
Catawba	1	–	–	–	2	2	1	1	1	–	–	–	–	1	1												11.60
"Santee"									1	–	–	–	1									..					15.00
saludae	1	1	–	–	1	1	5	3	5	7	6	11	7	7	14	3	6	6	3	1	–	–	–	–	1		16.87

ptures have been made only in Singletary d White lakes. Based upon present data, e lakes may be ranked with the number fish species present as the criterion as llows: Black; Jones; Salters; Singletary; /hite; Waccamaw.

Meager data for a third type of biological timate of productivity are available. In e course of fishery investigations upon e Bay Lakes made by D. E. Louder, two ore rotenone collections of a half acre ch were made during the summers of 57, 1958 and 1959 in each of the lakes 959 collections omitted in Black Lake). ne mean pounds of fish per acre from ese samples is included in Table 28. These lues are used with some hesitation for veral reasons. Two samples per lake, per ar, especially in a lake as large as Wacmaw, can not adequately represent the oductivity of the lake. Secondly, the riations between the pairs of collections om Waccamaw are so great as to make e value of these quantities dubious. Nevtheless, ranking the lakes by this method ves the following order: Black; Jones; ngletary; Salters; and Waccamaw and /hite.

If the three biological characters are nked in the same manner as the physicalemical factors, the lakes fall into the me order (Table 29). Plotting the mean mber of pored lateral-line scales alongde of the physical-chemical and biological dices of productivity (Table 29) shows em to be correlated. White and Waccaaw appear to be reversed, but the differce between these two (as well as between nes and Salters) is not of great signifince because differences of this magnitude greater occur between most isolated pulations. What is the significance of is correlation? Is this correlation caused some effect of the environment upon ese fishes?

To answer these questions the development of the pored lateral-line scales was udied (see development of *E. f. fusirme*). The development of pored lateralne scales in the Long Island population Fig. 11) and in White Lake (Fig. 12) similar except that in White Lake there e a few adults 23 and 24 mm long that ve retained the juvenile condition of a duced number of pored scales.

When the data for Jones Lake are examined (Fig. 13) a different picture is revealed. The no-pored condition is present until about 16 mm as in the two preceding cases, but here the transition period is never completed. Some of the largest specimens examined lacked pored lateral-line scales. It is apparent that here too the number of pored scales does not change after maturity; the whole range of variation has merely been shifted to lower values. Since this population retains into maturity the juvenile, no-pored condition, or at least a reduced number of pored scales, it can be considered a case of neoteny. In other words, there is a relative retardation in the rate of development of the body as compared with the reproductive organs, so that the body does not go through as many steps in development in the ontogeny of the descendants as it did in that of the ancestor (de Beer, 1951).

What has caused neoteny in the dark Bay Lakes populations of *Etheostoma f. fusi-*

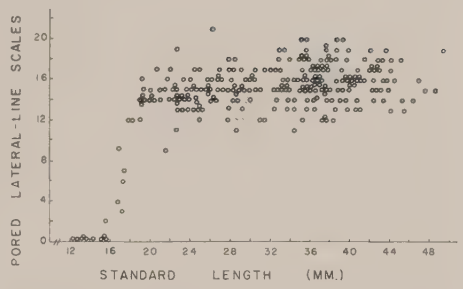


Figure 11. Change in the number of pored lateral-line scales with size in *Etheostoma fusiforme fusiforme* from two ponds on Long Island, New York.

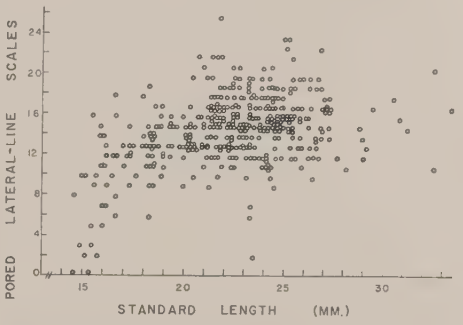


Figure 12. Change in the number of pored lateral-line scales with size in *Etheostoma fusiforme fusiforme* from White Lake, North Carolina.

forme? Hubbs (1926) discussed the results of changes in developmental rate and noted that accelerated development might lead to the retention of juvenile characters. In the dark Bay Lakes, under conditions of reduced productivity, selection may have acted to favor populations capable of spawning at a younger age or smaller size because of the relative scarcity of food. If populations could reproduce at smaller sizes they would be favored because of the food economy effected. Thus, selection could gradually reduce the size of the *E. fusiforme* in the dark lakes and result in a reduced number of pored lateral-line scales. Hubbs (1926) noted that degeneration resulting from a change in developmental rate does not primarily or necessarily involve any genetic loss, but involves physiological adaptations which preclude the completion of certain ontogenetic processes. Evidence is not yet available to determine whether or not the reduced number of pored scales in the dark Bay Lakes is genetically controlled or is a direct result of the environment. However, there is no significant difference between the number of pored lateral-line scales between the 1947, 1958, and 1959 year classes (see section IV) indicating that direct environmental control is unlikely. Linder (1958: 205-206) noted that *E. spectabile* and *E. spectabile* x *radiosum* hybrids, raised from eggs laid in the laboratory failed to develop any pored lateral-line scales. It would be interesting to raise *E. fusiforme* from the light and dark Bay Lakes for several generations to discover if there is genetic control for this neotenic character.

There is still more evidence for the neoteny theory. Examination of the variation in the number of pored lateral-line scales in *E. fusiforme barratti* (Table 19) shows that a few populations of this subspecies also have a reduced number of pored lateral-line scales. The over-all mean for *f. barratti* pored lateral-line scales is 20.65, while the mean of a population of *f. barratti* from Crystal Lake, Ga. is only 6.06. This lake is surrounded by the Suwannee River drainage although it lacks both inlet and outlet. The mean number of pored lateral-line scales in the Suwannee population is 22.41. Thus, in the Suwannee drainage, there is an even greater difference than between the dark and light Bay Lakes. Crystal Lake, Ga. is *not* a dark stained l as are the unproductive Bay Lakes. only apparent similarity between these la is their poor productivity. Donald C. Sc (personal communication) described Cr tal Lake as "one of a number of sink h lakes in Georgia which is filled with be tiful white sand and crystal clear wat the latter would double well for the c tilled product. Crystal Lake has no in or outlet, its water obviously is rainwa that has percolated through nothing m than clean sand. The water of the lake no contact with the underlying limest responsible for the basin. The carbon content is only about 15 p.p.m., vegetat is sparse, plankton likewise." Two coll tions (UG 205, 205a) were made on M 5, 1951, and April 26, 1952, and only 13 s cies of fishes were taken. Interestingly (Ta 30) the first six species listed are part the core of 11 species present in the L Lakes. The next three were found in least one dark and one light la *Notemigonus* was taken only in Lake W camaw. Only the last three species w not taken in the Bay Lakes. If Crys Lake is placed in the ranked Bay La series it ranks at about the same level Salters Lake. (This results from rank the alkalinity as 1, the aquatic vegetat as 3, the light penetration as 6, and number of species as 2, for a total of while Salters equals 11.5.) Because Crys Lake is clear, water color is eliminated a sole cause of the difference in num of pored lateral-line scales between dark and light Bay Lakes. However, co is important because of its great effect reducing productivity by limiting photos thesis. This is supported by the fact that *E. f. fusiforme* from Ellis Lake, North Ca lina, have a normally high number of po lateral-line scales ($\bar{x}$:13.31 vs. an over mean for *E. f. fusiforme* of 13.96). Th as Bailey and Frey (1951:202) noted, a dark, shallow lake with a low pH and l concentration of chemically active s stances. They also pointed out (p. 19 that "Ellis Lake has large fish populatio and might be even more productive unit area (or volume) than Waccama Once again it is productivity that is c related with the number of pored late line scales.

Several other populations of *E. f. barr*

ad unusually low numbers of pored lateral-ne scales (Table 19). One of these is from canal between Alligator and Lizzie lakes ear St. Cloud, Osceola Co., Florida UMMZ 158641). These two lakes are onnected, by canal only, with the St. Johns iver system. The mean of a sample from ie St. Cloud population is 13.42, while iat of the St. Johns population is 22.68. ollections are available from a number of nall isolated lakes in and around Orlando, lorida. These also have a low mean num-er of pored lateral-line scales ($\bar{x}$: 16.76). lowever, in this case some lakes seem to ave normal populations, others intermed-te forms. There are collections from the ake Okeechobee drainage which also have reduced number of pored lateral-line ales ($\bar{x}$:17.33). Here the range is 5 to 0 in adult specimens. There is a tempta-on to cite these cases as additional cor-boration of the neoteny theory, but un-rtunately no information was available n the productivity of these lakes.

If the low number of pored scales in ie dark Bay Lakes has arisen independently rough neoteny in each of these lakes, ien the populations in the Cape Fear iver, which is presumably more produc-ve, should have a higher count similar to ie specimens from productive White ake. I tried to collect specimens in Turn-ull Creek, which receives drainage from oth Jones and White lakes. The localities ined were moderately fast streams for the oastal Plain and no *E. f. fusiforme* were ollected. However, specimens were avail-ble from various localities in the Cape ear River. The majority of these are aratypes of Hubbs and Cannon's *"thermo-hilum"* taken from the region around Wil-ington, N.C. These specimens plus sev-ral small Cornell collections (Table 19) ow a count ($\bar{x}$: 14.07) which is closer to iat of the White Lake population than iat of the dark Bay Lakes populations. robably the river was originally populated y a form with a normally high number f pored scales. Some individuals were able o make their way into each of the Bay akes (except Black Lake?) where popu-tions built up quite rapidly. Then, in ach of the dark lakes, the scarcity of food aused selection to favor the development f neotenic populations.

Dorsal Spines (Table 20): The range is eight to thirteen, with the mode usually ten. Six *E. f. fusiforme* populations have a mode of nine and one (Nantucket) has a mode of eight spines. Eight dorsal spines was the primary character of which Hubbs and Cannon (1935:83) based their *f. insulae*. The Nantucket population is quite different from the Cape Cod and other Massachusetts populations in this regard. However, the Weweantic River, which is just west of Cape Cod, has a population with a mode of nine, bridging the gap between nominal *metaegadi* and *insulae*. The other five populations of *E. f. fusiforme* with a modal number of nine are: Raritan, N.J.; Nansemond, Va.; and the three dark N.C. Bay Lakes (Singletary, Salters, Jones). This seems to be a separate system of variation, not connected with neoteny, because both the neotenic and normal populations of *E. f. barratti* have modes of ten dorsal spines (except for the Red River population, which has a mode of eleven).

Dorsal Rays (Table 21): There is a range of eight to thirteen and the mode is either ten or eleven. The variation is slightly different from that in other characters. Populations of *E. f. fusiforme* seem to alternate geographically between modes of ten and eleven. All *E. f. barratti* populations from the Savannah southward have a mode of eleven. The Pee Dee, Edisto, and Combahee-Broad populations have modes of ten like adjacent *E. f. fusiforme*, indicating that the break between the Waccamaw and Pee Dee rivers is not as complete as in other characters.

Scale rows above the lateral line (Table 22): The range is two to four, with one specimen from coastal Maryland having

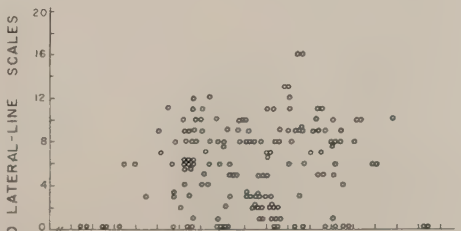


Figure 13. Change in the number of pored lateral-line scales with size in *Etheostoma fusiforme fusiforme* from Jones Lake, North Carolina.

five scales. The mode of most populations of both subspecies is three. The only populations of *E. f. fusiforme* with a mode of two are lakes Ellis, Salters, Jones, White, and Waccamaw. This was one of the characters used by Hubbs and Cannon (1935) in distinguishing *thermophilum.* However, the other North Carolina Bay Lake (Singletary) has a population with the normal mode of three scales. The reason for this is as yet unknown; the more productive Bay Lakes (White, Ellis, and Waccamaw) all have a reduced number.

Several populations of *E. f. barratti* also have a mode of two: St. Cloud, Fla.; Orlando, Fla.; and Crystal Lake, Ga. This is of interest because these populations are neotenic with regard to pored lateral-line scales. The reduction in number of pored lateral-line scales is correlated with the reduction in the number of scales below the lateral line. Perhaps the low productivity in these lakes has led to a reduction in several different characters.

Scale rows below the lateral line (Table 22): The range in *E. fusiforme* is six to twelve scales. The mode in the majority of populations is either eight or nine scales. There are three populations of *E. f. fusiforme* and two of *E. f. barratti* that have a mode of only seven: Ellis, Salters, other Cape Fear, Crystal Lake, Ga., and Orlando, Fla. The other four North Carolina Bay Lakes populations (Singletary, Jones, White, and Waccamaw) all have a more typical mode of eight. St. Cloud, Fla., Lake Okeechobee, Fla., and the Santee River, S.C., are the only populations of *f. barratti* with modes of eight; the first two are neotenic with regard to pored lateral-line scales. This character shows the same trend as the scales above the lateral line. If these two numbers are added together (Table 22) most populations have a total greater than 10.5 in *E. f. fusiforme* and greater than 11.2 in *E. f. barratti.* The populations with the lowest total number are neotenic and partially neotenic ones: Ellis Lake, N.C. (9.23); Salters Lake (9.65); other Cape Fear (9.65); Waccamaw (9.85); and in *E. f. barratti,* St. Cloud (10.28); Orlando (9.48); Lake Okeechobee (10.55); and Crystal Lake (9.36).

Anal Spines (Table 42): There is no significant variation in anal spines; almost all *E. fusiforme* have two. Seventeen specimens of *E. f. fusiforme* and eight of *E. barratti* had only one spine while two specimens of *E. f. barratti* had three spines.

Anal rays (Table 23): The range in character is five to ten with the mode either seven or eight, except for the Nannan Lake, Fla. population which has a mode of nine. Bailey (1950) gave a modal number of eight anal rays for his *Hololepis barratti appalachia* versus a modal value seven for other *barratti* populations. However, as Table 23 shows this is hardly basis for describing a new subspecies.

Pectoral Rays (Table 23): The range 12 to 15 with the majority of specimens of both subspecies having 13. The Crystal Lake, Ga. population stands out with range of 14 to 15 and a mode of 15. Perhaps this difference is negatively correlated with the reduced number of pored lateral line scales present in this population; however, the other neotenic populations typically have the usual mode (13).

Branchiostegal Rays (Table 44): The range of this character was from five seven with the majority of specimens having six rays. The few Cape Cod specimens examined showed a slight tendency to have more specimens with five rays. There was not sufficient variation in this character to necessitate presenting the frequency distributions by river systems, so summaries of both subspecies are presented in comparison with the other forms studied.

Interorbital Pores (Table 45): All the *E. f. fusiforme* examined lacked interorbital pores, but a few specimens of *E. f. barratti* had one or two pores present.

Infraorbital pores (Table 24): There were 11 different combinations of the pores in the

Figure 14. Percent of individuals with 1 + 3 infraorbital pores by river system from north to south in *Etheostoma fusiforme.*

anal. They have been arranged across he table in the order of increasing numers of pores in both segments of the canal. nce there were only two major categories 1 + 3 and 2 + 3), the infrequent counts ere added to the more similar of the two equent counts and the percentage of 1 + individuals in each population was comted.

The number of infraorbital pores was ed by Hubbs and Cannon (1935:30) to fferentiate *fusiforme* and *thermophilum* 2+3) from *barratti* (1 + 3). The present udy confirms this with 80% of *E. fusirme fusiforme* having 2 + 3 pores and 0% of *E. fusiforme barratti* having 1 + 3 ores (Table 24).

Bailey and Frey (1951) used the numer of infraorbital pores to distinguish their *ermophilum oligoporum* (1 + 3) in the rk North Carolina Bay Lakes from *thermophilum thermophilum* (2 + 3) in the ghter Bay Lakes. The present study conms these differences: the dark Bay Lakes ve a high percent of individuals with + 3 pores (Singletary-77%, Salters-83%, nes-97%); the light Bay Lakes a low perntage (White-17%, Waccamaw-9%). If ese percentages are plotted against the dices of productivity (Table 29), it can seen that the two numbers are even more osely correlated than in the case of the red lateral-line scales. The population *E. f. fusiforme* in the Cape Fear River oper has a percent (7%) much closer the White Lake population than to the pulations in the dark Bay Lakes. Therere, it appears that under similarly unoductive conditions in each of the dark y Lakes, selection (or the environment?) s acted to produce a form with a reduced mber of infraorbital pores as well as a duced number of pored lateral-line scales. is Lake has 47% of its individuals with + 3 pores and so falls in between the rk and light Bay Lakes in this charac-. The populations of *E. f. barratti* with duced numbers of pored lateral-line scales of less help in this situation because normal number for this subspecies is + 3. All the populations with reduced mbers of pored lateral-line scales have higher percent of 1 + 3 pores than do populations from which they are probly derived: Crystal Lake, Ga., population (92%) compared with the surrounding Suwannee population (57%), St. Cloud, Fla. (97%) and the surrounding St. Johns population (86%), and Orlando, Fla. (91%) and the St. Johns population (86%).

One peculiar population of *E. f. barratti* (Ogeechee, Ga.) has an abnormally low percent (7%) of individuals with 1 + 3 pores. Some of the western populations of *E. f. barratti* (Table 24) have 100% 1 + 3 pores (Pearl-Pontchartrain, La. and Red River) as does also the population from the French Broad (*"barratti appalachia"*).

Condition of Preopercle (Table 24): Hubbs and Cannon (1935:29-30) char-

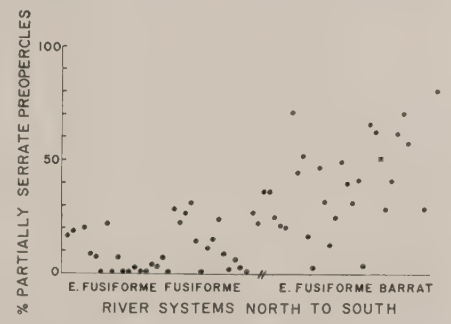


Figure 15. Percent of individuals with partially serrate preopercles by river systems from north to south in *Etheostoma fusiforme*.

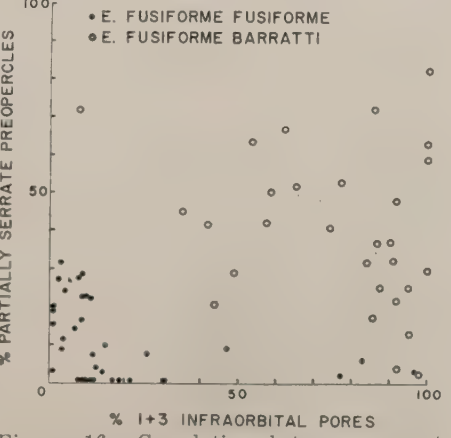


Figure 16. Correlation between percent of individuals with 1 + 3 infraorbital pores and percent of individuals with partially serrate preopercles by river systems in *Etheostoma fusiforme*.

acterized all the species of the subgenus *Hololepsis,* except *serriferum,* as having the "preopercle strictly entire." Bailey (1950: 315) has shown that *E. fusiforme barratti* has some serrae on the preopercle. This was one of the main characters that he used to distinguish his *Hololepis barratti appalachia.* There is a tendency toward a partially serrate preopercle in most populations (Table 24). This character can be used to divide *E. fusiforme* into two subspecies. Most populations of *E. f. fusiforme* have less than 25% of the specimens with serrae present while most populations of *E. f. barratti* have serrae in more than 25%. There is a tendency for the percentage to increase southward, with a break between the Pee Dee and Waccamaw rivers (Fig. 16). There are a number of exceptions that must be discussed.

In all of the North Carolina Bay Lakes except the Waccamaw population (23%) there is a much lower percent than would be expected (0% in White to 9% in Ellis Lake). Several *E. f. barratti* populations also have low percentages. Three of these are at least partially neotenic with regard to the number of pored lateral-line scales: Crystal Lake, Ga. (4%), St. Cloud, Fla. (3%), and Okeechobee, Fla. (13%). The Orlando populations do not show this tendency as they did in the number of pored lateral-line scales. A few typical *E. f. barratti* populations also have a low percentage of individuals with partially serrate preopercles: St. Johns, Fla. (17%), Savannah (20%), Red (17%), and Combahee-Broad (21%). Here is one more case where the North Carolina Bay Lakes are similar to some of the Florida and Georgia populations. It seems unlikely that these similarities are merely coincidental. Somehow the reduced productivity in all these lakes has acted, or is acting to influence these characters.

There is an interesting relationship between the percentage of individuals with partially serrate preopercles and the percent of individuals with 1 + 3 infraorbital pores: both percentages tend to increase to the south (Figs. 14 and 15). Most *E. f. barratti* populations have high percentages in both characters. The populations which have a low percent of partially serrate preopercles have a high percent of 1 + 3 individuals. If one percentage is higher than usual in a population of *E. f. fusiforme* the other is then lower than usual. For example, dark Bay Lakes have a high percent 1 + 3 pores (77%, 83%, and 97%) the partially serrate percent is very (2%, 6%, and 3% respectively). S populations have the partially serrate cent relatively high, for example Poto (31%), Delaware River (28%), o Cape Fear (28%), and Chesapeake (27%) but the values of their 1 + 3 centages are low: 3%, 9%, 7%, and respectively. The percent of indivic having 1 + 3 infraorbital pores has plotted by populations against the per of individuals having partially serrate opercles in the same drainages. Most p lations of *E. f. fusiforme* are found a the edge of Fig. 16, below 25% part serrate preopercles and extending up nearly 100% 1 + 3 infraorbital pores w the populations of *E. f. barratti* are lim to the central portion of the figure.

Preoperculomandibular Pores (T 45): The range in *E. f. fusiforme* is to eleven; eight to ten in *E. f. barratti,* the mode always nine. Populations f both Raritan Bay, N. J. and White L N.C. have means (8.30 and 8.34) cor erably below the over-all mean (8.9).

Coronal Pore (Table 47): As Bailey Frey (1951:200) pointed out, this cha ter is difficult to use. They reported the pore was frequently absent in pop tions in White and Ellis lakes and pre in the other Bay Lakes populations. appears to be true although in the cas White Lake there were only a few specir in which the condition could be sati torily determined. In most other pop tions the pore was usually present, altho its development varied, sometimes bei rather long posterior-extending tube an external opening, and other times b just an opening at the junction of the medial sidebranches of the supraor canal. Perhaps further study of this would be of value.

Supratemporal Canal (Table 47): canal is typically complete in adult *E. forme* and incomplete in young and j niles (see development in *E. f. fusif* and *E. f. barratti*). Table 31 shows normal development in the Long Is population. There are differences betv populations. For example, Bailey Frey (1951:200) cited the incomplete

e of the supratemporal canal in the ngletary and Salters lakes populations as example of local variation in a charac-. Development in Jones Lake (Table 31) like that in the Long Island population cept that it is completed at a smaller e. The transition period is longer (ten n) in both White and Singletary lakes Table 31); than in the Long Island and nes Lake populations (six mm). Since ere are so few large specimens it is doubt-l if the transition is ever completed. The nsition period in the Waccamaw popu-ion is lengthened to 14 mm. The most treme condition is present in Salters Lake, ere the transition period is entirely en-osed by the juvenile period, the largest ecimens having incomplete supratemporal nals.

Since the development of the supra-mporal canal is retarded relative to the owth of the gonads in the Salters, Wac-maw, Singletary, and White populations, ese populations may be considered neo-nic in this character. The Crystal Lake, a. population that was neotenic in the mber of pored lateral-line scales shows e usual development of the supratemporal nal (Table 31 and development in *E. fusi-rme barratti).*

Squamation: The value of squamation as a xonomic character was indicated by Hubbs d Cannon (1935) in their analysis of the ecies of *Hololepis.* They gave only general scriptions of squamation characterizing *fusiforme* as "interorbital scaleless, or ith one or two more or less imbedded ales," *thermophilum* as "interorbital with veral ctenoid scales," and *barratti* as "in-rorbital well covered with ctenoid scales." hey further differentiated *barratti* from *siforme* and *thermophilum* with the for-er having "parietals covered well toward across median line with ctenoid scales" d the other two forms as having "parie-ls scaleless." Hubbs and Cannon described ly the general trends. More quantitative ethods were devised, as discused in sec-on III. The squamation of the preopercle, ercle and nape is usually 100-X-T, so equency distributions for the subspecies e summarized in Table 48. However, there e significant differences in the squama-on of the breast, parietal, and interorbital.

Breast Squamation (Table 25): In the northern part of the range of *E. fusiforme* the breast squamation is usually 100-I-C, with the amount of exposure and the tendency to become ctenoid increasing to the south. In the North Carolina Bay Lake populations, specimens were found to have all the intermediate conditions (I/PX-C/T, PX-T, and X/PX-T) between imbedded cycloid scales (I-C) and exposed ctenoid scales (X-T). Most specimens in populations south of the Waccamaw River have the squamation at least I/PX-C/T. West of the Apalachicola River, Fla. the breast is usually PX-T or even X-T in the case of the Pearl-Pontchartrain, La. and Red River populations.

Parietal Squamation (Table 26): This character shows the differentiation between the two subspecies more clearly than does the breast squamation. In the northern part of the range of *E. f. fusiforme,* most specimens have naked parietals. The amount of squamation gradually increases toward the south. Of the North Carolina Bay Lakes, the Singletary Lake population has the parietal squamation the least well developed (mostly 5-10%) and the White Lake population has the squamation the best developed (mostly 25-30%). There is a break between the Waccamaw (15-20%) and Pee Dee (35-40%). The variation in this character is greater in *E. f. barratti* (5-100%) than in *E. f. fusiforme* (0-50%). The range within populations is also considerably greater in the southern subspecies (5-95% in the St. Mary's, based on only 12 specimens) than in the northern subspecies (15-60% in White Lake). This tendency has been noted for a number of other characters, in particular the interorbital squamation *(q.v.).*

Interorbital Squamation (Table 27): The range in *E. f. fusiforme* is 0-12 (mode 0, $\bar{x}$: 1.97), while that of *E. f. barratti* is 1-37 scales (mode 10, $\bar{x}$: 13.15) (Table 46). This difference seems to be sufficient to divide the species into two subspecies but does not seem great enough, because of the wide overlap, to merit specific recognition. The north-south clinal nature of the variation in *E. f. fusiforme* is clearly demonstrated in the table. There is a gap between Waccamaw on the north and the Pee Dee River on

the south. There seems to be more intrapopulation and relatively less interpopulation variation in *E. f. barratti.*

2. Taxonomic Conclusions

Etheostoma fusiforme is the most variable species of the subgenus *Hololepis.* There are two ways to treat this variation: to name all distinguishable populations; or to describe the variations and try to understand them without the use of names. Minor differences beween populations should not be formally recognized because of the great plasticity of some characters in fishes. A number of environmental factors effect some meristic characters in some fishes. Perhaps the most important of these is the effect of water temperature on such characters as the number of vertebrae and fin rays (Tăning, 1952; Blaxter, 1956; and others).

There are four patterns of variation in the characters studied in *Etheostoma fusiforme.* First, there are the characters that showed little or no variation; number of anal spines, anal rays, preoperculomandibular pores, interorbital pores, pectoral rays, pelvic rays, caudal rays, branchiostegals, and the squamation of the preopercle, opercle, and nape. In the second type, characters vary from population to population in an apparently random fashion (total lateral-line scales, dorsal spines, and dorsal rays). The third type is clinal; the breast, parietal, and interorbital show increasing development of squamation from north to south. The percent of individuals with $1 + 3$ infraorbital pores and with partially serrate preopercles also increases from north to south. The fourth type is the most interesting: the incomplete development of some characters (neoteny) in populations in the unproductive North Carolina Bay Lakes and in a few Florida and Georgia lakes. This has been noted in the greatly reduced number of pored lateral-line scales, the failure of the supratemporal canal to become closed, the reduced number of scales above and below the lateral line, and the percentage of individuals with $1 + 3$ infraorbital pores.

The major taxonomic problem was to decide which populations merit nomenclatorial recognition. I believe the differences between Hubbs and Cannon's three species, *fusiforme, thermophilum,* and *barratti,* are due to clinal variations (squamation, infraorbital pores, deve ment of the pored lateral line) and to d opmental variations (infraorbital pores pored scales in *thermophilum*). The species of *fusiforme* recognized by Hu and Cannon (1935) were based on a c bination of: random variations ((lateral-line scales in *fusiforme insulae f. metaegadi* and dorsal spines in *fusifo insulae*) and clinal variations (interor squamation in three groups: *f. atra* and *f. erochroum; f. fusiforme* and *f. me gadi; f. insulae*). This was coupled the improper presentation of counts f both sides of individuals (see section and inadequate sampling between the ra of the forms they recognized. J. R. Bai *barratti appalachia* is almost certainly b upon an introduced population (Ba Winn, and Smith, 1954). It is slightly ferent in having a higher percentage specimens with partially serrate preoper The most interesting case is surely *ther philum oligoporum.* It seems clear that form in the dark North Carolina Bay L has differentiated independently in each probably as a result of the unproduc conditions in these lakes. Thus all the species of *E. fusiforme* and of *E. ther philum* are reduced to synonymy unde *fusiforme fusiforme* while *E. barratti E. barratti appalachia* become *E. fusifo barratti.*

Etheostoma saludae (Hubbs and Cannon)

Hololepis saludae—Hubbs and Can 1935:50-52, pl. I-III (original descriptio Fowler, 1945:40, 196 (Saluda Co., S. C Freeman, 1952a:37 (Broad R., Richl Co., S. C.).

Etheostoma saludae—Bailey and Gosl 1955:20, 44 (number of vertebrae); Ec 1957:220; Moore, 1957:198; Collette, 19 2051.

Types—Holotype, UMMZ 107079; mm juvenile; S. C., Saluda Co., Richl Cr., trib. to Lake Murray, 10 mi. SE Saluda; June 21, 1933; E. M. Burton. P types, the other 16 specimens examined Hubbs and Cannon (1935:50).

Diagnosis—One or two anal spines; b interorbital pores usually present; in orbital pores either $1 + 4$ or $1 + 3$; n squamation usually less than 60% ($\bar{x}$: 15%

TABLE 33.
Number of total lateral-line scales in Etheostoma collis and E. saludae

rm and drainage	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	$\bar{x}$
lis lepidinion																	
Roanoke					3	1	7	5	2	5	2*	3	4				43.00
Neuse	1	2	1	–	2	–	1										37.57
Cape Fear												1**					–
lis collis																	
Yadkin-Pee Dee						1	1	1	6	8	3	5	4	–	1		44.50
Rocky-Pee Dee						1	–	2	3	4	4	1	2	3	1		44.86
Catawba			1	–	1	1	1	1	1	–	2	1					42.00
"Santee"								1	1								42.50
udae		1	2	8	8	11	12	10	17	9	7	1	1	1	1	1	41.78

Count of holotype of *E. c. lepidinion*.
This specimen counted on right side.

ast naked. Maximum size of males 42.5 n SL. (CU 35019) and females 43.5 mm U 35029).

Coloration—Hubbs and Cannon's (1935: 52) description was based entirely upon mature specimens (17-22 mm). No adult n-breeding males were available to me, t they probably are similar to the females. e pigmentation of *E. saludae* is similar to t of *E. collis*.

The spinous dorsal fin of the non-breeding nale has few to a moderate number of all to medium sized melanophores scat-ed on the membrane. The soft dorsal fin barred on the rays and rectangular blotches nposed of 10-15 melanophores are pres- on the membranes. The anal fin is clear has a few small melanophores on the oximal portion of the membranes. The ctoral fin membranes are clear, but me-ophores outline the rays. The pelvic fin, ly, and breast lack pigment. The caudal barred. There are large and small melano-ores scattered on the cheek. The sub-ital, preorbital, and postorbital bars are prominent. The pored portion of the eral line is light. The median basi-caudal t is prominent; dorsal and ventral spots sometimes present. The sides are irreg-rly mottled with brown; up to eight eral blotches may be present. The genital pilla is unpigmented. Most specimens e about seven dorsal saddles, two before first dorsal fin, two under each dorsal and one posterior to the second dorsal

Some breeding females have more melano-ores on the second dorsal fin membranes n do non-breeding females. The anal fin gmentation varies, even within a single collection, from immaculate to a moderate number of melanophores scattered over the membrane. Figure 17 shows the pattern of a breeding female *E. saludae* compared with *E. collis*.

Most parts of the body and fins of the breeding males are colored like the females; other areas are darker. The spinous dorsal has more melanophores; they are concentrated on the first two or three membranes, and there is a tendency toward a median band. The second dorsal fin has about 30-40 melanophores in each rectangular blotch. The anal and pelvic fins and the belly and breast are uniformly covered with small to medium melanophores. The cheek is darker in the male than in the female. The suborbital bar is more prominent in some breeding males. There is more pigment on the distal edges of the pored lateral-line scales. Dorsal saddles and blotches are usually absent. Figure 18 compares the patterns of breeding males of *E. collis* and *E. saludae*.

Genital Papilla—A moderately elongate blunt tube in breeding females. A specimen taken on April 1 (CU 25982) has a genital papilla 1.5 mm long and 0.9 mm thick at the base. The genital papilla is like that of *E. f. fusiforme* (Fig. 1f).

Breeding Tubercles—Present on anal and pelvic fins. Males taken on April 16 (CU 35019) have tubercles on most of the ventral surface of pelvic rays one to four and along the distal seven-eighths to three-quarters of the anal rays. The tubercles on the anal rays are somewhat larger than those on the pelvic rays. Another collection taken on March 14 (CU 35036) contains a male with large tubercles on the distal three-quarters of anal rays one and two

TABLE 34.

Condition of supratemporal canal and the number of pores in the infraorbital, interorbital, and preoperculomandibular canals in Etheostoma collis and E. saludae

Form and drainage	Infraorbital				Interorbital			Preoperculomandibular						Supratemporal	
	2+4	1+4	1+3	2+3	0	1	2	6	7	8	9	10	11	Incomplete	Complete
c. lepidinion															
Roanoke		29*	3		31*	1				2	27*	1	1	23*	8
Neuse		5	2		6	1				1	6				7
Cape Fear		1			1						–			1	
c. collis															
Yadkin-Pee Dee		2	28	1	23	1	2	1	–	3	19	3		20	11
Rocky-Pee Dee		1	28		24					1	22			5	19
Catawba			11		11						10	1		9	2
"Santee"		1	1		2						2			1	1
saludae	1	59	34			3	90			3	85	2		53	41

* Count of holotype of *E. c. lepidinion*.

TABLE 35.

Number of anal rays and of scale rows above and below the lateral line in Etheostoma collis and E. saludae

Form and drainage	Anal Rays					Above			Below lateral line						
	6	7	8	9	x̄	2	3	4	6	7	8	9	10	11	x̄
c. lepidinion															
Roanoke	1	7	20*	4	7.84	8	23*	1		1	11*	11	7	2	8.94
Neuse	1	3	3		7.29		7			1	3	3			8.29
Cape Fear		1			–			1			1				–
c. collis															
Yadkin-Pee Dee		2	20	9	8.23	6	24	1		7	12	12			8.16
Rocky-Pee Dee		13	10	1	7.50	3	13	2			12	7	3		8.59
Catawba		3	7	1	7.82	2	5	1			5	4	–	1	8.70
"Santee"			2		8.00		2						2		10.00
saludae	1	18	64	10	7.89	25	67		1	19	37	29	6		8.22

ure 17. Breeding patterns of female *Etheostoma collis* and *E. saludae*. (upper) *E.* s LEPIDINION, paratype; CU 29992; 38.6 mm; Va., Charlotte Co., Roanoke dr.; Mar. 1956. (middle) *E. collis collis;* CU 11988; 41.3 mm; N.C., Davidson Co., Yadkin-Pee dr.; Mar. 22, 1958. (lower) *E. saludae;* CU 35030; 40.7 mm; S.C., Saluda Co., Sa- dr.; Apr. 16, 1954. (Photograph by Douglass M. Payne)

on the distal three-quarters of all the ic rays where the tubercles are scattered smaller. This is essentially the same dis- ution as found in *E. collis collis* (Fig. 1g).

Habitat—Field notes of E. C. Raney for spring collections (CU 17542, 25966, 82, 26061) indicate the habitat to be ll woodland streams, 5-15 feet wide, feet deep, with a flow of 5-10 cubic per second, current slow to moderate, the bottom consisting of sand, gravel, bedrock.

Distribution — Limited to Piedmont ams of the Saluda and Broad Rivers, ch are tributaries of the Congaree, the southern branch of the Santee River in South Carolina. Figure 3 shows the distribution of the collections examined.

Specimens Examined—Saluda-Broad Dr., S.C.—Laurens Co.: CU 19745 (1, 39); Bush Cr. 1.5 mi. SW of Kinards on SC 560; March 28, 1951. Lexington Co.: CU 35035 (3, 30-41); Kinley Cr. 2 mi. S of Irmo, ½ mi. W SC 36; March 18, 1954. CU 35024 (6, 25-38); CU 35026 (6, 25-37); SC 36 1 mi. W of US 76; March 27, 1954. CU 35027 (1, 37); SC 20, 1 mi. S of Little Mt.; March 27, 1954. CU 25966 (1, 32); Rawl Cr., 2 mi. S of Kino on SC 107, trib. ½ mi. from Saluda R.; April 1, 1954. CU 25982 (12, 25-39); trib. of Saluda R. about 1 mi. from Saluda R., 2 mi. S of Irmo on SC sec. 36; April 1, 1954. Newberry Co.: CU 35029 (1, 44); Timothy Cr. SC 42, 2 mi. W of Prosperity; Feb. 20, 1954. CU 35037 (1, 42); Garrison Cr. SC 58, 6 mi. SW Kinards; Aug. 5, 1954. Richland Co.: CU 26061 (14, 28-42); Nicholas Cr. trib. of Broad R. 4.5 mi. S of Broad R., 6 mi. SE Ballentine on SC sec. 129; April 1, 1953.

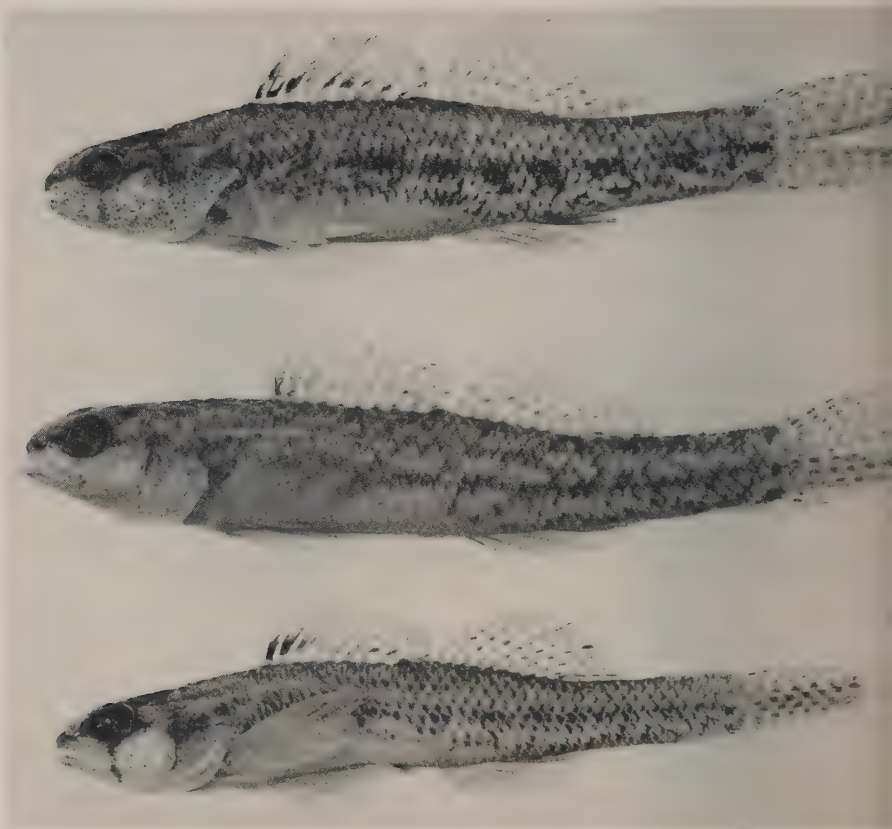


Figure 18. Breeding patterns of male *Etheostoma collis* and *E. saludae.* (upper) *collis* LEPIDINION, holotype; USNM 179847; 37.6 mm; Va., Charlotte Co., Roanoke Mar. 31, 1956. (middle) *E. collis collis;* CU 31663; 39.5 mm; N.C., Stanly Co., Roc Pee Dee dr.; Mar. 31, 1958. (lower) *E. saludae;* CU 35030; 34.9 mm; S.C., Saluda Saluda dr.; Apr. 16, 1954. (Photograph by Douglass M. Payne)

Saluda Co.: UMMZ 107077 (4, 17-21); Moore's Cr., trib to Lake Murray, 6 mi. SE of Saluda; June 21, 1933; paratypes. UMMZ 107078 (2, 20-22), USNM 94685 (1, 22), Chicago Nat. Hist. Mus. 38331 (1, 17), out of Charleston Mus. 33.149.1, paratypes and UMMZ 107079 (1, 21) holotype of *Hololepis saludae;* Richland Cr., trib. to Lake Murray, 10 mi. SE of Saluda; June 21, 1933. CU 17542 (15, 28-40); trib. of Little Saluda R., 2.1 mi. N of Saluda on rt. 19; March 23, 1950. CU 35023 (1, 32); 1 mi. NE Cherry Hill School, 7 mi. E of Saluda on SC 192; Oct. 16, 1953. CU 35033 (2, 29-31); Richland Cr., 4 mi. E of Saluda on SC 43; Oct. 16, 1953. CU 35032 (2, 37-38); Moore's Cr., 3 mi. W of Batesburg on SC 57; Mar. 14, 1954. CU 35031 (1, 40); Clouds Cr., 3 mi. N of Ridge Spring on SC 57; Mar. 14, 1954. CU 35036 (3, 32-40); Mine Cr., 6 mi. S of Saluda on SC 193; March 14, 1954. CU 35022 (3, 31-36); S branch of Red Bank Cr., 5 mi. SW of Saluda on SC 84; April 6, 1954. CU 35034 (1, 36); S branch of Big Cr. on SC 83 at Trinity Church, 5 mi. NW of Saluda; April 6, 1954. CU 35021 (1, 37); Ready Cr., ½ mi. E of Ready Cr. School, 5 mi. N of Ward; April 16, 1954. CU 35019 (3, 33-43); N branch of Mine Cr., 3 mi. N of Ward on SC 193; April 16, 1954. CU 35030 (6, 33-43); S. branch of Red Bank Cr., on SC 186, 5 mi. SW of Saluda; April 16, 1954. 35020 (2, 25-28); a south branch of Red B Cr., SC 84 at Salem Church, 5 mi. W of Salu April 16, 1954. CU 35028 (1, 39); Big Cr., 5 NW of Saluda Shiloh Church on SC 39; Apri 1954. CU 35025 (2, 31-36); Little Saluda R mi. NE of Saluda on SC 39; Oct. 16, 1954.

Etheostoma collis **lepidinion** *subsp. n*
Etheostoma collis new subspecies—C lette, 1961:2051.

Types—Holotype, USNM 179847; 3 mm male; Va., Charlotte Co., trib. of Ho pen Cr., 2.4 mi. NW of Wylliesburg Va. 607; March 31, 1956; Raney, C lette, New, Cole, Robins; ECR 2787 BBC 160. One of a series of nine sp mens (CU 29992). Paratypes are all other specimens examined except for 25187 from the Cape Fear River.

TABLE 36.

Squamation of the nape, breast, preopercle, and opercle in Etheostoma collis and E. saludae

Form and drainage	Percent of Nape Scaled												Percent of Breast Scaled									
	0	10	20	30	40	50	60	70	80	90	100	$\bar{x}$	0	10	20	30	40	50	60	70	80	$\bar{x}$
c. lepidinion																						
Roanoke									2	4	26*	97.5		3	5	5	6*	6	3	3	1	40.3
Neuse								1	–	3	3	91.4		2	–	1		1	2	–	1	42.9
Cape Fear										–		–										–
c. collis																						
Yadkin-Pee Dee	26	1	1									1.1	28									0
Rocky-Pee Dee	18	5	–	1								3.3	24									0
Catawba	6	1	1	1								6.7	9	1								1.0
"Santee"	–											–	2									0
saludae	32	30	14	10	1	2	1	–	1	3		15.2	91	2								.2

Form and drainage	Percent of Preopercle Scaled									Percent of Opercle Scaled												
	30	40	50	60	70	80	90	100	$\bar{x}$	0	10	20	30	40	50	60	70	80	90	100	$\bar{x}$
c. lepidinion																						
Roanoke								32*	100.0											32*	100.0
Neuse								7	100.0											7	100.0
Cape Fear								1	–											1	–
c. collis																						
Yadkin-Pee Dee			1	1	–	1	2	19	94.6	2	–	–	1	–	–	–	1	2	1	20	87.0
Rocky-Pee Dee								24	100.0										2	16	98.9
Catawba								8	100.0				1	–	1	–	–	–	1	4	81.4
"Santee"									–												–
saludae	1	2	–	1	–	–	6	74	96.5				1	1	–	1	1	8	27	30	90.9

* Squamation of holotype of *E. c. lepidinion*.

Diagnosis—Similar to *E. collis collis* in having one anal spine and usually lacking both interorbital pores. Differs from *E. c. collis* and *E. saludae* in having the breast at least partially covered with scales ($\bar{x}$: 41%). Differs from *E. c. collis* by usually (88%) having 1 + 4 rather than 1 + 3 infraorbital pores. Differs from both *E. saludae* and *E. c. collis* in having the nape well scaled (80-100%, $\bar{x}$: 96%), while *E. c. collis* has less than 20% of the nape scaled and *E. saludae* usually has less than 60% scaled. Maximum size of males 37.7 mm, females 40.1 mm (both from CU 34544, Roanoke R.).

Counts of the holotype (with one asterisk) and paratypes are given in Tables 32-36 in comparison with *collis collis* and *saludae*. The three forms are compared in Table 37.

The relationships of this form with *E. collis collis* and *E. saludae* are discussed above in Section VI.

Etymology—The name *lepidinion* is derived from the Greek (*lepis,* scale) and (*inion,* nape) in allusion to the diagnostically scaly nape.

Coloration—The female has a few scattered melanophores on the first dorsal fin, mostly on the spines. The second dorsal fin has a few large melanphores on the membranes. The anal fin is clear in most specimens; sometimes with a few melanophores scattered on the rays. The pelvic fin is clear. The caudal fin membranes are clear; large brown or black chromatophores are present on the rays. The belly, breast and usually the lower sides are free of melanophores. The cheek has a few large scattered melanophores. The preorbital and postorbital bars are well developed; the suborbital is usually faint; the supraorbital is usually absent. The pored portion of the lateral line is clear. There is usually a median spot at the division the upper and lower caudal rays, and fa spots at the base of the upper and lo portions of the caudal fin. About ei lateral blotches are present and are m distinct posteriorly. The genital pap is immaculate. Figure 17 compares pattern of a breeding female *E. collis lep inion* with *E. collis collis* and *E. saludae*

The anal, pectoral, pelvic and cau fins, orbital bars, basi-caudal spots, and pored portion of the lateral line in the n breeding male are colored like the fem other areas are darker. Many small mela phores form a median band on the me brane of the first dorsal fin. The sec dorsal fin differs from that of the fem in having rectangular patches of sm melanophores on the membranes. Both belly and breast are covered with slight moderate numbers of small melanopho The cheek is darker. The lateral blotc are slightly more distinct in some ma than in the females. There is a narr band of small melanophores around base of the genital papilla.

In the breeding male the pectoral caudal fins, orbital bars, and genital pap are colored like the non-breeding m the other areas are darker. The en spinous dorsal fin is covered with sm melanophores. These are concentrated dially and form a band which is especi prominent on the first three membra The rectangular blotches in the soft do fin are each composed of about 25 (15-5 melanophores, and these blotches tend form bands across the fin. The anal pelvic fins, belly, breast and cheeks completely covered with small mela phores. The pored portion of the lat line is prominent because of the dark sid some pigment is present on the distal p tions of the pored lateral-line scales,

TABLE 37.
Differential characters of the forms of Etheostoma collis and E. saludae

Form	*collis lepidinion*	*collis collis*	*saludae*
River system	Roanoke, Neuse	Pee Dee, Catawba	Saluda, Br
Infraorbital pores	1+4 (90%)	1+3 (95%)	1+4 (65% 1+3 (35%
Interorbital pores	0 (95%)	0 (95%)	2 (95%
Nape (% scaled)	80-100%	Less than 20%	Usually le than 60%
Breast (% scaled)	10-80%	naked	naked
Anal spines	always I	always I	II (70% I (30%

rupting the narrow light line. The dian basi-caudal spot is prominent; the rsal and ventral ones diffuse. The sides ually show less distinction between the rker blotched portion below the lateral e and the lighter upper portion. Figure 18 is a comparison of the pattern of a breeding male with *E. collis collis* and *E. saludae*.

Genital Papilla—The genital papilla of the breeding female is a moderately elongate tube like that of *E. fusiforme* (Fig. 1f).

TABLE 38.

umber of total lateral-line scales in the species of the subgenera Hololepis and Villora

ecies	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
lolepis																			
erriferum													1	—	—	3	8	11	27
racile									3	12	21	27	34	79	91	123	130	89	70
oniferum										2	1	—	—	2	1	6	7	5	1
f. barratti											2	8	16	28	39	72	121	132	165
f. fusiforme									1	5	12	20	46	64	118	152	226	220	229
saludae					1	2	8	8	11	12	10	17	9	7	1	1	1	1	1
c. lepidinion				1	2	1	—	5	1	8	5	2	5	2	4	4			
c. collis						1	—	1	3	2	5	11	12	9	7	6	3	2	
llora																			
okaloosae	1	6	24	34	13	1													
edwini			4	12	79	217	189	91	35	14	3								

ecies	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	N	$\bar{x}$
ololepis																		
serriferum	32	40	42	41	46	36	24	28	7	12	1	3	2	1	—	1	366	54.05
gracile	68	33	24	4	2												810	47.60
zoniferum	1	1	1														28	47.46
f. barratti	165	158	138	102	66	60	51	29	17	10	5	3	2				1389	51.37
f. fusiforme	234	198	160	124	65	66	31	14	13	6	—	2					2006	50.18
saludae																	90	41.78
c. lepidinion																	40	42.13
c. collis																	62	44.19
llora																		
okaloosae																	79	34.70
edwini																	644	37.67

TABLE 39.

Number of pored lateral-line scales in the species of the subgenera Hololepis and Villora

ecies	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
ololepis																			
serriferum														2	20	24	49	78	101
gracile								1	—	—	1	—	1	2	3	6	2	4	3
zoniferum	4	1	5	4	2	3	3	4	7	7	7	13	12	24	32	61	57	89	106
f. barratti	11	7	12	11	8	14	23	23	34	46	53	113	182	300	300	320	235	172	92
f. fusiforme						1	1	—	—	1	1	5	3	5	7	6	11	7	7
saludae											1	—	1	5	4	6	5	3	7
c. lepidinion						1	—	—	—	3	5	6	5	9	5	7	7	4	4
c. collis																			
llora																			
okaloosae																			
edwini																			

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
ololepis																			
serriferum		1	—	2	1	1	2	3	5	14	20	25	28	21	34	41	40	33	26
gracile	140	120	121	61	45	23	13	14	3										
zoniferum	3	2																	
f. barratti	74	116	111	105	107	84	84	76	58	24	23	17	11	6	3	5	—	1	3
f. fusiforme	68	42	21	15	5	3	—	1											
saludae	14	3	6	6	3	1	—	—	—	—	1								
c. lepidinion	1	1	1	1															
c. collis	1	1	3	1	1	1	—	—	—	—	—	1							
llora																			
okaloosae												3	4	19	27	19	6	2	
edwini		2	5	9	23	48	62	101	112	97	48	40	22	20	5	4			

	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	N	$\bar{x}$
ololepis																	
serriferum	24	5	13	3	2	2	—	2								348	33.66
gracile																844	19.53
zoniferum																28	15.61
f. barratti																1349	20.65
f. fusiforme																2111	13.96
saludae																89	16.87
c. lepidinion																36	15.89
c. collis																65	14.66
llora																	
okaloosae																80	33.01
edwini																598	27.02

Breeding Tubercles—Present on the pelvic and anal fins of breeding males. Specimens taken on March 31 (CU 29992) have moderately large tubercles on the lower side of the spines and rays of the pelvic fins and on all the anal fin rays. Their distribution is similar to that in *E. collis collis* (Fig. 1g).

Habitat—Field notes for two Roanoke River localities (CU 29992 the type locality, and CU 34544) show the habitat to be backwater pools of small streams with a depth of 2-4 feet, width of 10-20 feet, flow of about three cubic feet per second, banks partly wooded, current slow to moderate, bottom sand overlain with some mud and with thin to thick layers of detritus.

Distribution—Like its relatives, *E. collis collis* and *E. saludae, E. c. lepidinion* is limited to Atlantic Piedmont streams. This is the most northern of the three forms and is found in the Roanoke and Neuse Rivers. The juvenile specimen from the Cape Fear River is referred to this subspecies with some question so it remains to be determined whether the range extends that far south. Figure 3 shows distribution of the collections of this f that have been examined.

Specimens Examined—All specimens designated as paratypes except for the gle specimen from the Cape Fear.

Roanoke, R., Va.—Charlotte Co.: US 100215 (3, 29-31); Wards Fork, trib Roanoke R., S of Madisonville; April 1935. USNM 101330 and 101334 (12, 29); Wards Fork, Roanoke Cr., below dam, between Madisonville and Cullen; S 15, 1935. USNM 179847 (1, 38) holo and CU 29992 (8, 30-38); trib. of Ho pen Cr., 2.4 mi. NW of Wylliesburg Va. 607; March 31, 1956. CU 34544 29-40); Wards Fork Cr., 6.7 mi. SSW Madisonville on Va. 47; Sept. 16, 1 N.C.—Granville Co.: DU uncat. (1, Beech Cr., 3 mi. NNE of Cornwall (area now flooded by Kerr Dam); Sp 1952.

Eno-Neuse R., N.C.—Durham Co.: uncat. (5, 30-35); 4.5 mi. E Oak Gr Lick Cr. on rt. 264; April 9, 1950. Ora Co.: DU uncat. (1, 36); Eno R. 2

TABLE 40.
Number of unpored lateral-line scales in the species of the subgenera Hololepis and Villora

Species	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Hololepis																		
serriferum													2	5	4	14	18	30
gracile																		
zoniferum																		
f. barratti																	1	2
f. fusiforme																		
saludae																		
c. lepidinion																		
c. collis																	1	—
Villora																		
okaloosae	5	33	26	12	4													
edwini					5	10	11	24	50	97	95	121	70	50	56	17	9	5
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Hololepis																		
serriferum	39	44	33	25	24	15	25	10	13	2	1	2	—	—	2	1	—	—
gracile	1	2	4	9	17	32	64	88	123	118	113	76	49	36	30	12	7	2
zoniferum							1	1	1	—	3	3	3	5	1	6	1	1
f. barratti	8	6	12	16	41	51	53	77	83	101	120	103	100	108	95	70	56	65
f. fusiforme					2	3	1	4	16	26	35	65	84	111	132	155	181	190
saludae	2	3	10	2	14	9	14	8	7	4	2	4	3	1	—	—	1	—
c. lepidinion			2	2	3	2	5	6	4	5	2	3	—	1	1			
c. collis	—	—	—	1	—	5	1	1	5	3	6	13	8	4	—	4	6	2
Villora																		
okaloosae																		
edwini																		

	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	N
Hololepis																
serriferum																346
gracile																785
zoniferum	1															28
f. barratti	20	22	20	19	11	12	4	3	2	3	2	1	—	—	1	1333
f. fusiforme	150	144	119	103	54	32	25	13	12	2	9	5	2	3	1	1862
saludae																87
c. lepidinion																36
c. collis																60
Villora																
okaloosae																80
edwini																621

TABLE 41.
Number of first dorsal spines and second dorsal rays in the species of the subgenera Hololepis and Villora

Species	Spines									Rays											
	7	8	9	10	11	12	13	N	$\bar{x}$	8	9	10	11	12	13	14	15	16	17	N	$\bar{x}$
Hololepis																					
serriferum			3	48	227	88	1	367	11.10				1	22	137	167	37	2	1	367	13.62
gracile	3	69	506	240	11	1	2	832	9.24		2	106	454	244	25	1				832	11.22
zoniferum		3	11	8	6			28	9.61		1	10	14	3	1					29	10.76
f. barratti		12	141	605	288	12		1058	10.14	3	41	324	503	177	9					1057	10.79
f. fusiforme		76	418	689	251	45	2	1481	9.85	2	73	563	686	141	7					1472	10.62
saludae		12	68	12				92	9.00				5	48	37	2				92	12.39
c. lepidinion		7	28	5				40	8.95				4	19	16	1				40	12.35
c. collis	1	3	55	9				68	9.06			1	21	38	8					68	11.78
Villora																					
okaloosae		2	31	4				37	9.05			3	32	40	5					80	11.59
edwini		52	368	149	4			573	9.18		7	175	296	89	7					574	10.85

TABLE 42.
Number of anal spines and rays in the species of the subgenera Hololepis and Villora

Species	Spines					Rays								
	1	2	3	N	$\bar{x}$	4	5	6	7	8	9	10	N	$\bar{x}$
Hololepis														
serriferum	1	368		369	2.00		6	77	196	85	5		369	7.02
gracile	22	817	1	840	1.98		6	313	468	51	1		839	6.68
zoniferum	3	26		29	1.90	1	8	13	7				29	5.90
f. barratti	8	1057	2	1067	1.99		1	57	400	472	124	2	1056	7.63
f. fusiforme	17	1445		1462	1.99		4	127	691	578	75		1475	7.40
saludae	28	68		96	1.71			1	18	64	10		93	7.89
c. lepidinion	40			40	1.00			2	11	23	4		40	7.73
c. collis	68			68	1.00				18	39	11		68	7.90
Villora														
okaloosae		37	1	38	2.03			8	65	7			80	6.99
edwini	5	541	1	547	1.99		5	195	286	58	3		547	6.74

TABLE 43.
Number of scale rows above and below the lateral line in the species of the subger Hololepis and Villora

Species	Above the Lateral Line 2	3	4	5	6	N	
Hololepis							
serriferum		17	286	55		358	
gracile	3	289	453	66	1	812	
zoniferum		22	7			29	
f. barratti	157	776	100			1033	
f. fusiforme	362	1042	48	1		1453	
saludae	25	67				92	
c. lepidinion	8	30	2			40	
c. collis	11	44	4			59	
Villora							
okaloosae		10	70			80	
edwini	5	304	245	8		562	

Species	Below the Lateral Line 5	6	7	8	9	10	11	12	13	14	15	N	
Hololepis													
serriferum						25	111	140	75	4	1	356	11
gracile			19	238	356	160	29	3				805	8
zoniferum			6	12	9	2						29	8
f. barratti		1	61	286	456	200	26	2				1032	8
f. fusiforme		28	299	723	361	35	2	1				1449	8
saludae		1	19	37	29	6						92	8
c. lepidinion			2	15	14	7	2					40	8
c. collis			7	29	23	5	1					65	8
Villora													
okaloosae	5	74										79	5
edwini	7	150	246	114	36	8	1					562	7

TABLE 44.
Number of branchiostegals and pectoral rays in the species of the subgenera Hololepis and Villora

Species	Branchiostegals 5	6	7	N	
Hololepis					
serriferum	3	138	9	150	6
gracile	10	177	8	195	5
zoniferum		11	2	13	6
f. barratti	15	134	4	153	5
f. fusiforme	31	150	3	184	5
saludae	1	30	2	33	6
c. lepidinion		30	2	32	6
c. collis		34	1	35	6
Villora					
okaloosae		10		10	6
edwini	1	98	7	106	6

Species	Pectoral Rays 10	11	12	13	14	15	N	
Hololepis								
serriferum		13	118	26			157	12
gracile			2	158	13		173	13
zoniferum			3	17	2	1	23	13
f. barratti			26	125	47	11	209	13
f. fusiforme			9	155	36	1	201	13
saludae		40	47				87	11
c. lepidinion		2	28	3			33	12
c. collis	1	29	31	1			62	11
Villora								
okaloosae			16	52	6		74	12
edwini		2	45	91	3		141	12

TABLE 45.
Number of preoperculomandibular pores and interorbital pores in the species of the subgenera Hololepis and Villora

	Preoperculomandibular pores								
ecies	6	7	8	9	10	11	12	N	$\bar{x}$
olepis									
erriferum		2	24	322	6			354	8.94
racile			5	64	718	22	1	810	9.94
oniferum				2	23			25	9.92
. barratti			37	919	20			976	8.98
. fusiforme	5	21	149	1201	20	2		1398	8.87
aludae			3	85	2			90	8.99
. lepidinion			3	33	1	1		38	9.00
. collis	1	–	4	53	4			62	8.95
lora									
kaloosae			1	46	4			51	9.06
dwini			11	163	366	7		547	9.67

	Interorbital Pores				
ecies	0	1	2	3	N	$\bar{x}$
olepis						
erriferum	33	67	255		355	1.63
racile	786	15	3		804	.03
oniferum	29				29	0
. barratti	1026	3	2		1031	.01
. fusiforme	1427				1427	0
aludae		3	90		93	1.97
. lepidinion	38	2			40	.05
. collis	65	1	2		68	.07
lora						
kaloosae	1	2	44		47	1.91
dwini	7	33	493	1	534	1.91

of Hillsboro; March 20, 1949. DU cat. (1, 38); Eno R. at ford N of Hillsro near Skipper Wright's; April 21, 1955. Cape Fear R., N.C.—Guilford Co.: CU 187 (1, 20); Haw R., 3.5 mi. S of kesdale on rt. 68; June 24, 1946.

Etheostoma collis collis
(Hubbs and Cannon)

Hololepis collis—Hubbs and Cannon, 35: 52-54, pl. I-III (original descripn); Fowler, 1940:40 (Santee R.); Ranl, 1958: 342 (Piedmont of S. C., Catawb-Wateree R.).

Etheostoma collis—Bailey and Gosline, 55: 20, 44 (number of vertebrae); ore, 1957:198.

Etheostoma colle—Eddy, 1957: 220.

Etheostoma collis collis—Collette, 1961: 51.

Types—Holotype, UMMZ 94560; 40 n male; S. C., York Co., creek near York; v. 11, 1931; Donald Ameel, Paratypes, MMZ 107085; same data as holotype and MMZ 94546; S. C., York Co., Steele Cr., . to Catawba R., Rock Hill; Nov. 11, 31, Donald Ameel.

Diagnosis — One anal spine (erroneously given as two on the types by Hubbs and Cannon, 1935:53); interorbital pores usually absent; usually (93%) 1 + 3 infraorbital pores; nape squamation usually less than 20% ($\bar{x}$: 3%); breast naked. Maximum size of males 43.1 mm SL (CU 31663, Rocky-Pee Dee R.), females 43.0 mm (CU 33052, Yadkin-Pee Dee R.).

Coloration—All the available collections contain specimens with at least a vestige of breeding color. There are no important differences between the breeding patterns of *E. collis collis* and *E. collis lepidinion*. There are probably few differences between the patterns of non-breeding individuals. Hubbs and Cannon's (1935) description of males taken in November indicated the breeding pattern. Breeding males do not have a red submarginal band in the first dorsal fin as postulated by Hubbs and Cannon (1935).

The breeding female has small melanophores scattered on the anterior spines, and has large and small melanophores on the posterior spines of the first dorsal fin. The second dorsal has rounded patches of me-

TABLE 46.

Number of infraorbital pores and interorbital scales in the species of the subgenera Hololepis and Villora

Species	Complete Infraorbital							Interrupted Infraorbital										N	Usual Number	
	4	5	6	7	8	9	10	0+2	0+3	1+2	1+3	1+4	2+2	2+3	2+4	3+3	3+4			
Hololepis																		358		6.16
serriferum		1	6	290	56	5												808		7.95
gracile				2	101	648	53	4							2	21	—	2	25	84%	2+4
zoniferum									18	7	976	15	3	364	7	5			1395	70%	1+3
f. barratti								1	10	6	298	2	6	1381	8	19	1		1732	80%	2+3
f. fusiforme											34	59	—	—	1				94	63%	1+4
saludae											5	35							40	88%	1+4
c. lepidinion											63	4	—	1					68	93%	1+3
c. collis																					
Villora																					
okaloosae					2	39													41		7.95
edwini			1	39	480	24	1												545		7.97

Species	Interorbital Scales																																			N	$\bar{x}$
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37		
Hololepis																																							148	16.6
serriferum							3	2	7	6	8	1	4	13	9	16	11	7	15	6	4	5	10	6	3	1	3	1	1	1	1	1	1	1	—	1			116	0
gracile	116																																						14	0
zoniferum	14																																					1	267	13.2
f. barratti		1	1	1	1	7	7	9	17	19	26	25	19	14	24	16	18	17	10	6	11	4	4	2	—	3	1	1	—	—	1	1	—	—	—	—	—	—	306	2.0
f. fusiforme	76	72	64	43	24	7	9	6	2	1	1	—	1																										46	0
saludae	46																																						13	0
c. lepidinion	13																																						35	0
c. collis	35																																							
Villora																																							10	0
okaloosae	10																																						85	0
edwini	85																																							

TABLE 47.
Supratemporal canal and coronal pore and condition of preopercle in the species of the subgenera Hololepis and Villora

ecies	Coronal Pore		Supratemporal Canal	
	Present	Absent	Complete	Incomplete
olepis				
erriferum	47		346	3
racile	455	2	715	48
oniferum	6		8	21
. barratti	342	24	1201	84
. fusiforme	305	55	1047	122
aludae	45		41	53
. lepidinion	32		15	24
. collis	37		33	35
lora				
kaloosae	46		43	3
dwini	259		516	20

ecies	Condition of Preopercle			
	Entire	Partly serrate	Serrate	N
lolepis				
erriferum			304	304
racile	772			772
oniferum	29			29
. barratti	900	515		1414
. fusiforme	1620	194		1814
aludae	96			96
. lepidinion	35	5		40
. collis	68			68
lora				
kaloosae	3	14*	28*	45
dwini	518	2		520

* The preopercle is crenulate instead of serrate in *E. okaloosae*.

ophores that tend to form bands across fin. The anal fin is clear in most ecimens, while others have concentrans of small melanophores. The pectoral s of both males and females have lanophores on the rays. The pelvic fin ks melanophores. The caudal is barred. e breast, belly and lower sides lack lanophores. There are scattered large lanophores on the cheek. In both sexes re are usually three orbital bars present; orbital, preorbital, and postorbital. The st two are the most prominent and some ecimens lack the postorbital as well as the raorbital. The pored portion of the lateral e stands out as a narrow light line alough it may be interrupted by some pigent under the distal third of the scale. e median basi-caudal spot is the most ominent although it is diffuse in some ecimens. The dorsal and ventral spots y in intensity, and are sometimes alst as prominent as the median spot. st females have variegated brown sides d lack lateral blotches. The genital pala lacks pigment. The patterns of breeding females of *E. collis collis, E. collis lepidinion* and *E. saludae* are compared in Figure 17.

As in *E. collis lepidinion,* the breeding male is colored like the female, but darker in some regions. The membranes of the first dorsal fin are covered with small melanophores concentrated on the anterior three membranes. Some specimens have the first membrane almost entirely black. Four to five sets of quadrangular blotches give the second dorsal a banded appearance. The anal fin, belly and breast are uniformly covered with small melanophores. There are more small melanophores on the membranes than on the rays of the pelvic fin. The cheek has more melanophores than that of the female. Males usually have seven to eight lateral blotches which extend from the caudal base to the middle of the first dorsal fin. These blotches are more prominent in the smaller adults. There is pigment on the posterior ventral side of the genital papilla in large males. Some small specimens have a band of pigment encircling the papilla. A specimen

TABLE 48.

Squamation of breast, nape, parietal, preopercle and opercle in the species of the subgenera Hololepis and Villora

Breast

	Percent						Almost entirely 100%						
	0	10-20	30-40	50-60	70-80	90-100	I-C	I/PX-C/T	PX-C/T	PX/X-T	X-T	N	x̄
Hololepis													
serriferum							107	41	3	1		152	70% I-C
gracile	129											129	0
zoniferum	14											14	0
f. barratti							23	78	57	23	52	233	33% I/PX-C/T
f. fusiforme							156	49	18	18	6	247	63% I-C
saludae	91	2										93	.2%
c. lepidinion		10	12	12	5							39	41%
c. collis	63	1										64	.2%
Villora													
okaloosae			1	10	4							15	59%
edwini	2	1	9	22	16	52						102	76%

Nape

	Percent						Almost entirely 100%						
	0	10-20	30-40	50-60	70-80	90-100	I-C	I/PX-C/T	PX-C/T	PX/X-T	X-T	N	x̄
Hololepis													
serriferum									3	13	88	104	85% X-T
gracile	10	24	12	7	14	93						160	70%
zoniferum	12	2										14	1%
f. barratti								3	19	46	111	179	62% X-T
f. fusiforme								12	39	57	70	178	39% X-T
saludae	32	44	11	3	1	3						94	15%
c. lepidinion					3	36						39	96%
c. collis	50	9	2									61	3%
Villora													
okaloosae							5	26	1			32	81% I/PX-C/T
edwini							3	43	23	13	18	100	43% I/PX-C/T

Preopercle

	Percent						Almost entirely 100%						
			30-40	50-60	70-80	90-100	I-C	I/PX-C/T	PX-C/T	PX/X-T	X-T	N	x̄
Hololepis													
serriferum											99	99	100% X-T
gracile							1	3	6	26	126	162	78% X-T
zoniferum								4	4	5		13	38% PX/X-T
f. barratti									1	6	155	162	96% X-T
f. fusiforme								4	6	59	113	182	62% X-T
saludae			3	1	–	80						84	97%
c. lepidinion						40						40	100%
c. collis				2	1	53						56	98%
Villora													
okaloosae								23	5	2		30	77% I/PX-C/T
edwini								7	13	30	53	103	51% X-T

Opercle

	Percent						Almost entirely 100%						
	0	10-20	30-40	50-60	70-80	90-100	I-C	I/PX-C/T	PX-C/T	PX/X-T	X-T	N	x̄
Hololepis													
serriferum											99	99	100% X-T
gracile							1	10	28	55	68	162	42% X-T
zoniferum											14	14	100% X-T
f. barratti								4	1	25	139	169	82% X-T
f. fusiforme								4	9	23	158	194	81% X-T
saludae			2	1	9	57						69	91%
c. lepidinion						40						40	100%
c. collis	2	–	2	1	3	44						52	90%
Villora													
okaloosae										1	31	32	97% X-T
edwini								16	17	17	53	103	51% X-T

Parietal

	Percent						Almost entirely 100%						
	0	5-20	25-40	45-60	65-80	85-100	I-C	I/PX-C/T	PX-C/T	PX/X-T	X-T	N	x̄
Hololepis													
serriferum							2	82	27	26	17	154	53% I/PX-C/T
gracile	129											129	0
zoniferum	14											14	0
f. barratti		17	57	47	55	46						222	57.5%
f. fusiforme	105	144	19	4								272	9.5%
saludae	46											46	0
c. lepidinion	12											12	0
c. collis	36											36	0
Villora													
okaloosae	10											10	0
edwini	83	2										85	0

TABLE 49.

...mber of vertebrae in the species of the subgenera Hololepis and Villora (based in part on data presented by Bailey and Gosline, 1955)

...cies	33	34	35	36	37	38	39	40	41	N	$\bar{x}$
...olepis											
...rriferum						3	14	7	1	25	39.24
...racile				4	15	13	2			34	37.38
...niferum				1	3	4	2			10	37.70
...barratti					3	13	16	1		33	38.45
...fusiforme					5	25	15	8		53	38.49
...ludae				3						3	36.00
...lepidinion			2	7	5	2				16	36.44
...collis			1	1	1					3	36.00
...ora											
...kaloosae	1	10	13	2						26	34.62
...dwini		1	3	4	10	3				21	36.52

...mall as 27.4 mm has full breeding pig...tation and tubercles. A comparison of ...breeding pattern of male *E. collis collis*, *...collis lepidinion* and *E. saludae* is pre...ed in Fig. 18.

...enital Papilla—The genital papilla of ...breeding female is an elongate tube like ... of *E. fusiforme* (Fig. 1f).

...reeding Tubercles—Present on the anal ... pelvic fins of breeding males. Speci...s taken on March 22 (CU 11988) have ...derately large tubercles on the lower ... of the pelvic spine and rays and on ...he anal fin rays (Fig. 1g).

...labitat—Field notes for five late March ...ections (CU 29832, 29991, 31663, ...17, 33052), show the habitat to be ...ll to medium-sized streams, shore wood...or partly wooded and partly pasture, ...th 5-40 feet, depth 2-3 feet, current ...y to moderate, aquatic vegetation ab..., bottom sand, mud, or rubble covered ...n silt and/or detritus. All specimens ...e taken either in backwater pools or ... stream banks in slow-moving water. ...st of the specimens in one collection ...U 31663) were taken from the shallow ...er along the banks of a pool at a cattle ...sing; here a number were resting in ...ressions made by cows' hoofs, sheltered ...n the current. In Waxhaw Creek ...ek (CU 31717) three out of nine speci...s were taken near the banks of the main ...am over mud, while the other six were ...ected in a small backwater pool less ...n two feet wide.

...labits—Little is known of its habits. ...he spring of 1958, specimens from the ...kin River were brought back alive to ... laboratory. Although they survived a week-long collecting trip, they all died after being left in the laboratory for a few hours. Members of the *E. collis-saludae* complex live in the cooler and presumably more oxygenated waters of the Piedmont, so perhaps their oxygen requirements are higher than those of the lowland species of *Hololepis*, which are frequently taken in very warm stagnant situations. A few *E. serriferum* taken on this trip also died, but all the *E. fusiforme fusiforme* survived.

Courtship and spawning have not been observed. However, judging from the pigment pattern of the breeding males and the location of the breeding tubercles, it seems likely that the courtship patterns are similar to those of *E. f. fusiforme (q.v.)*. Eggs were extruded by a female collected on March 31 (CU 31663) when held in my hand, confirming the evidence from the breeding tubercle development that the spawning season is near the end of March.

Distribution—Restricted to the Piedmont streams of North and South Carolina. Taken only in two tributaries of the Pee Dee River (the Rocky and Yadkin rivers) and in the Catawba-Wateree branch of the Santee River (Fig. 3). The holotype and one of the paratypes were listed from an indefinite locality between the Catawba and Broad rivers (part of the Congaree-Santee system) but it is felt that these specimens must have come from the Catawba because the Saluda-Broad is inhabited by the closely related *E. saludae*.

Specimens Examined—Yadkin-Pee Dee R., N. C. Davidson Co.: all collections from the same locality which is: trib. of Yadkin R., 0.4 mi. W jct NC 109 and sec. rd., 1 mi. N of Cid: UMMZ 138569 (2, 31-33); UMMZ 138568 (1, 39); and CU 11988 (12, 27-41); March 22, 1948. Also CU 29991 (7, 31-38); March 30, 1956; and CU 33052 (9, 33-43); March 30, 1958.

Rocky R.-Pee Dee R., N. C.—Caborrus Co.: CU 19324 (1, 20); Rocky R. 5 mi. S of Odell; Oct. 13, 1946. Stanly Co.: CU 29832 (2, 35-36); trib. of Long Cr., 3.7 mi. N of Aquadale on sec. rd.; March 29, 1956. CU 31663 (21, 25-43); trib. of Rocky R. on dirt rd. between Red Cross and Locust (not NC 27); March 31, 1958.

Catawba-Santee R., N.C.—Union Co.: CU 35133 (1, 36); where a paved rd. from Waxhaw to NC 200 crosses Waxhaw Cr., 3.5 mi. SSE of Waxhaw; June 15, 1956. Same locality, CU 31717 (9, 22-38); March 31, 1958. S. C.—York Co.: UMMZ 94546 (1, 37); paratype; Steele Cr., trib. to Catawba R., Rock Hill; Nov. 11, 1931.

"Santee R." (Almost certainly Catawba-Santee), S.C.—York Co.: UMMZ 94560 (1, 40) holotype and UMMZ 107085 (1, 40) paratype; cr. near York; Nov. 11, 1931.

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X. ABSTRACT

The subgenus *Hololepis,* genus *Etheostoma,* includes eight forms of small specialized darters: four are found in the swamps, lakes, and backwaters of the Coastal Plain of eastern North America (*fusiforme fusiforme, fusiforme barratti, serriferum,* and *zoniferum*); one in the lowlands of the Mississippi Basin *(gracile);* and three in the backwaters of Atlantic Piedmont streams *(collis collis, collis* LEPIDINION new subspecies, *saludae). Etheostoma edwini* was replaced in the subgenus *Villora* Hubbs and Cannon.

E. serriferum is the most primitive species in the subgenus in virtually all characters: size, preopercular serrations, presence of interorbital pores, complete infraorbital canal, fairly complete lateral line, more fin rays, more complete squamation. It is divided into a northern and a southern race based on the number of interorbital scales, pored and total lateral-line scales.

E. gracile and *E. zoniferum* share a number of characters which show their close relationship: ten preoperculomandibular pores; interorbital pores absent; reduced squamation; green bars on the side; red spots in the dorsal fins and accessory breeding tubercles on the chins of males. The characters which differentiate *E. zoniferum* from *E. gracile* show that it is a specialized offshoot which has the squamation reduced and the infraorbital canal incomplete. *E. gracile* has as much variation inherent in each population as in the other species of *Hololepis,* but there has been little differentiation between populations.

The most variable species of the subgenus, and the one studied most intensively, is *Etheostoma fusiforme.* There are three types of variation in this species: (1) Variation from population to population in an apparently random fashion (*e.g.,* total lateral-line scales). (2) clinal variation shown in the increased development of squamation, the increased percent of individuals with 1+3 infraorbital pores and partially serrate preopercles; (3) variation in the retention of juvenile characters (neoteny). Neoteny was particularly evident in the greatly reduced number of pored lateral-line scales in the dark North Carolina Bay Lakes and in clear Crystal Lake, Georgia, both areas of low productivity. It was also noted in the failure of the supratemporal canal to become closed, in the reduced number of scales above and below the lateral line, and in the reduced number of infraorbital pores.

Etheostoma fusiforme, barratti, and *thermophilum* are shown to be conspecific; the differences between them are of clinal and developmental nature. The subspecies of *fusiforme* recognized by Hubbs and Cannon (1935) were based upon a combination of random variation, developmental variation, and clinal variation so *f. insulae, f. metaegas, f. erochroum,* and *f. atraquae* are synonymized with *f. fusiforme. Etheostoma thermophilum oligoporum* (J. R. Bailey and Frey) is considered to be based upon neotenic populations that have been produced independently in three of the dark North Carolina Bay Lakes. *Etheostoma thermophilum thermophilum* and *E. thermophilum oligoporum* are synonymized with *f. fusiforme. Etheostoma fusiforme fusiforme* differs from *E. f. barratti* in having fewer interorbital scales, less developed squamation of the breast and paretal, and fewer individuals with 1+ infraorbital pores and partially serrate preopercles. *Etheostoma barratti appalachia* (J. R. Bailey) is considered a slightly differentiated introduced population of *f. barratti* not worthy of subspecific recognition.

The *E. collis* group is the most specialized in the subgenus as shown in the reduction in number of pored and total lateral-line scales and vertebrae. *E. saludae* is more primitive than *E. collis*

in retaining the interorbital pores and having only about a third of the specimens with one anal spine. *E. collis* LEPIDINION is described from the Roanoke, Neuse, and Cape Fear rivers. It is more primitive than the nominate subspecies in having a scalier nape and breast and 1+4 instead of 1+3 infraorbital pores.

The paper includes a diagnosis of the subgenus *Hololepis;* keys to all forms; synonymies; pigmentation descriptions; range maps; photographs of all forms; drawings of breeding tubercles and genital papillae; discussions of habitat, associated species, habits, geographic variation, development, and evolutionary relationships.

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HEMIRAMPHUS BERMUDENSIS, A NEW HALFBEAK FROM BERMUDA, WITH A SURVEY OF ENDEMISM IN BERMUDIAN SHORE FISHES

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Abstract

A third species of *Hemiramphus* from the Atlantic, *H. bermudensis*, is described as a Bermudian endemic. It differs from *H. balao* LeSueur and *H. brasiliensis* (Linnaeus) primarily in having more gill-rakers. A survey of the approximately 70 forms of shore fishes originally known only from Bermuda indicates that 13 (about 4 per cent of the Bermudian shore fish fauna) are valid endemics.

Introduction

The purposes of this paper are to describe a previously unrecognized species of *Hemiramphus* endemic to Bermuda and to survey the endemic shore fishes of Bermuda. Additional information on this new halfbeak and the other Atlantic species of the Hemiramphidae will appear in a forthcoming volume of "The Fishes of the Western North Atlantic," and in an Atlantide report now in preparation.

I wish to thank Loren P. Woods, James E. Böhlke, and John E. Randall for providing me with unpublished data on the distribution of several species of fishes. Frederick H. Berry, James E. Böhlke, Daniel M. Cohen, J. A. F. Garrick, Robert H. Gibbs, Jr., Ernest A. Lachner, and Loren P. Woods have kindly read the manuscript and made valuable comments. The figure was drawn by Mildred H. Carrington.

Hemiramphus bermudensis new species

Hemiramphus braziliensis, Jones (*non* Linnaeus, 1785; this is an incorrect subsequent spelling of *H. brasiliensis*), 1859: 103 (listed as common).—Borodin, 1934: 109 (3 specimens from St. Georges).

Hemiramphus Pleii, Goode (*non* Valenciennes, 1846), 1876: 11 (taken in large numbers in Bermuda bays), 13 (listed as a species common to Bermuda, West Indies, and northern Brazil), 64 ("common gar-fish" seined in large quantities for the market, 2 sizes—about 20 inches and about 8 inches [the latter were probably *Hyporhamphus unifasciatus*]).—Jones, 1876: 135 (very common).—Goode, 1877a: 6 (listed).—Goode, 1877b: 292 (listed).

Hemiramphus brasiliensis, Barbour (*non* Linnaeus, 1785), 1905: 114 (MC 8774 taken at Bermuda about 1870).—Bean, 1906: 36 (CNHM 5051- 3 specimens from Hamilton and Somerset).—Beebe and Tee-Van, 1933 62 (common in Bermuda).

Diagnosis.—A species of *Hemiramphus* with a total of 37-45 gi rakers on the first arch (9-13+26-33); 12 to 14 anal rays; and moderate-sized pectoral fin, 5.2-6.7 times in the standard length.

Description.—Total gill-rakers on second arch 28-35 (5-10+21-28 dorsal rays 13-15, usually 14; pectoral rays 10-12, usually 11. Pe toral insertion to pelvic insertion 2.1-2.4 in standard length; pelv insertion to caudal base 2.8-3.0; lower jaw length (measured fro tip of upper jaw to tip of lower jaw) 3.1-3.6; pectoral length 5.2-5 in specimens 100-149 mm SL, 5.6-5.9 in specimens 150-221 mm

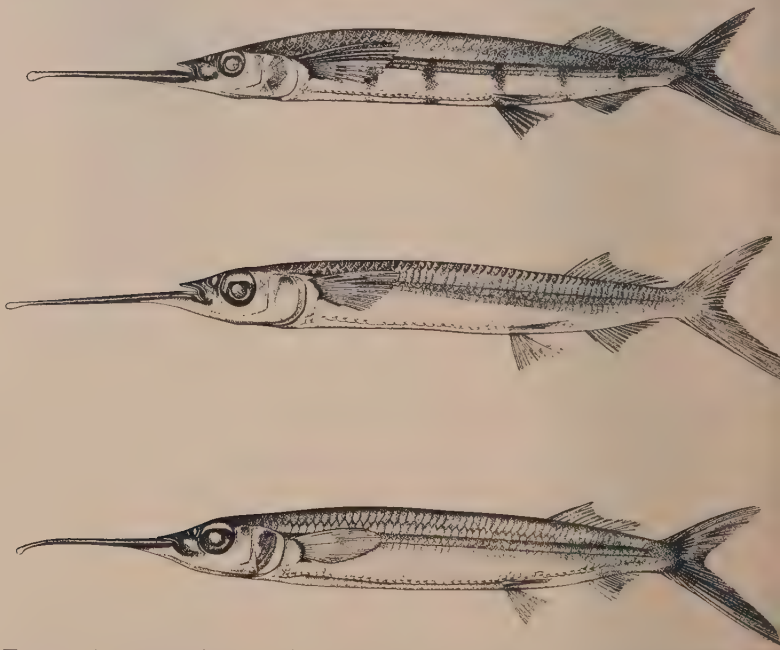

FIGURE 1. Comparison of juveniles of the three Atlantic species of *Hem ramphus.* Top: *Hemiramphus balao,* USNM 187566, 177 mm standard lengt M/V DELAWARE, 35°50′N, 72°35′W. Middle: *Hemiramphus bermudens* paratype, USNM 187565, 120 mm standard length, St. Georges Harbor, Be muda. Bottom: *Hemiramphus brasiliensis,* Bur. Comm. Fish. Biol. La Brunswick, Ga., M/V GILL 8, 119 mm standard length, Settlement Poi Grand Bahamas.

and 6.0-6.7 in specimens 226-300 mm SL; body depth at pectoral origin 7.3-8.5; depth at pectoral tip 6.0-8.7; depth at pelvic origin 8.2-9.1 in specimens 100-122 mm and 6.5-8.2 in specimens 137-300 mm. Otherwise conforming to the description of *Hemiramphus brasiliensis* as given by Miller, 1945.

Relationships.—*Hemiramphus bermudensis* appears to be an endemic Bermudian derivative of *H. brasiliensis* (Linnaeus), which is known from Woods Hole, Massachusetts, south through the West Indies and the Gulf of Mexico to Rio de Janeiro, and in the eastern Atlantic from Angola north to at least Dakar. *H. brasiliensis* has not been taken at or near Bermuda. *H. bermudensis* differs from *brasiliensis* primarily in having a greater number of gill-rakers (Table 1). Small juveniles of *bermudensis* (Bingham Ocean. Coll. uncat.) have fewer gill-rakers (35 and 34 in specimens 41.5 and 32.1 mm SL) than adults, but more than juveniles of *brasiliensis* (29-31 gill-rakers in specimens 32-50 mm SL). From *H. balao* LeSueur, the third Atlantic species of the genus, *bermudensis* differs primarily in its shorter pectoral fin (Table 3), greater number of anal rays (usually 13 versus usually 11-12, Table 2), and greater number of gill-rakers (37-45 versus 31-37). In number of gill-rakers, *bermudensis* is close to *H. saltator* Gilbert and Starks, of the eastern Pacific (gill-rakers 35-44), but differs from it by having a much shorter pectoral fin (5.6-6.7 times in standard length versus 4.4-5.1 in specimens over 150 mm SL). Of the four species of *Hemiramphus* mentioned, *bermudensis* has the least body depth, differing most strongly from *brasiliensis* in this regard (Table 3 and Fig. 1). *H. bermudensis* apparently attains a greater size than either *balao* or *brasiliensis*. With only 47 specimens of *bermudensis* available, 13 are over 250 mm, the largest about 310 mm SL. In many more specimens of *balao*, I have seen only four over 250 mm, the largest 270 mm, and of several hundred specimens of *brasiliensis*, only four are larger than 250 mm, the largest 272 mm.

Holotype.—Chicago Nat. Hist. Mus. 48115, from Whalebone Bay, St. Georges Island, Bermuda, June 22, 1948. Standard length 272 mm, lower jaw length 79.0 mm, pectoral fin length 42.5 mm, body depth at pectoral fin origin 35.6 mm, depth at pectoral tip 43.0 mm, depth at pelvic fin origin 41.0 mm, distance from pectoral fin origin to pelvic origin 125 mm, distance from pelvic fin origin to caudal base 93.5 mm. Dorsal rays 15, anal rays 12, pectoral rays 11. Gill-

TABLE 1

NUMBER OF GILL-RAKERS ON THE FIRST AND SECOND ARCHES (RIGHT SIDE) IN *Hemiramphus balao, bermudensis* AND *brasiliensis*.

FIRST ARCH

	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	$\bar{x}$
balao		1	—	1	14	18	18	32	18	9									34.37
bermudensis										5	7	4	7	7	6	3	—	1	40.00
brasiliensis	2	24	70	101	59	37	9	3	1										31.17

SECOND ARCH

	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35			$\bar{x}$
balao						2	5	12	7	1	1								27.11
bermudensis									1	6	9	9	10	2	—	2			30.95
brasiliensis	1	4	10	34	52	54	34	3	1	1									24.36

TABLE 2

NUMBER OF DORSAL AND ANAL RAYS IN *Hemiramphus balao, bermudensis* AND *brasiliensis*.

	Dorsal Rays						Anal Rays						
	11	12	13	14	15	$\bar{x}$	10	11	12	13	14	15	$\bar{x}$
balao	1	4	109	102	1	13.45	3	99	125	2			11.55
bermudensis			9	31	3	13.86			9	31	4		12.89
brasiliensis		2	118	254	15	13.73		1	115	292	11	1	12.75

rakers on first arch, right side 11+30=41, second arch 7+24=31.

Paratypes.—U.S. Nat. Mus. 21245 (1 spec., 244 mm SL); USNM 21884 (5, 157-297); USNM 187565 (3, 109-122); USNM 21377 (6, 187-300 + 3 heads of specimens that were about 150-190 mm); USNM 12699 (1, 263); Mus. Comp. Zool., Harvard 26718 (1, 219); Zool. Mus. Copenhagen 162 (1, 226); Chicago Nat Hist. Mus. 48490 (1, 137); CNHM 63878 (1, 167); CNHM 5051 (1, about 310); CNHM 5052 (1, 237); CNHM 5053 (1, 180); CNHM 48082 (1, 181); Univ. Michigan Mus. Zool. 175990 (1, 149); UMMZ 175982 (2, 161-175); UMMZ 172417 (7, 144-265); UMMZ 176512 (2, 210-255).

TABLE 3

PECTORAL FIN LENGTH AND BODY DEPTH IN *Hemiramphus balao, bermudensis* AND *brasiliensis* EXPRESSED AS TIMES IN STANDARD LENGTH.

Character and Size	*balao*			*bermudensis*			*brasiliensis*		
range (mm)	Range	$\bar{x}$	(N)	Range	$\bar{x}$	(N)	Range	$\bar{x}$	(N)
P_1 length									
100-149	4.6-4.9	4.73	(7)	5.2-5.7	5.42	(7)	5.5-6.0	5.78	(6)
150-199	4.5-5.2	4.94	(21)	5.6-5.9	5.73	(7)	5.3-6.0	5.66	(15)
200-300	4.8-5.4	5.08	(13)	5.7-6.7	6.36	(19)	5.6-6.4	5.97	(11)
Depth P_1 origin									
100-149	7.4-8.2	7.71	(7)	7.6-8.3	7.80	(7)	6.9-7.4	7.15	(6)
150-199	7.0-7.8	7.39	(19)	7.4-8.5	7.70	(7)	6.7-7.2	6.91	(14)
200-300	7.1-7.9	7.55	(12)	7.3-8.3	7.82	(20)	6.6-7.6	6.91	(12)
Depth P_1 tip									
100-149	6.3-7.3	6.97	(7)	6.6-8.7	7.51	(7)	6.2-6.8	6.49	(6)
150-199	6.3-6.7	6.51	(7)	6.0-7.1	6.56	(6)	5.8-6.3	6.04	(13)
200-300	6.0-7.0	6.51	(11)	6.0-8.0	6.90	(19)	5.5-6.4	6.01	(12)
Depth P_2 origin									
100-149	7.0-8.0	7.56	(6)	7.0-9.1	7.94	(7)	6.7-7.4	7.03	(6)
150-199	6.3-7.3	6.69	(16)	6.7-8.2	7.17	(7)	6.2-7.1	6.49	(13)
200-300	6.3-7.4	6.73	(12)	6.5-7.8	7.06	(19)	6.2-6.4	6.32	(4)

Other material examined.—Because of their small size, the following are not designated as paratypes of *H. bermudensis*: Bingham Ocean. Coll. uncat. (1, 32); BOC uncat. (1, 42); BOC uncat. (1, about 22 mm); CNHM 48769 (1, 30); UMMZ 176160 (1, 43); UMMZ 172422 (2, 19-20).

All of the material of *Hemiramphus balao, brasiliensis,* and *salta* in the following collections was examined: USNM, MCZ, UMM BOC, CNHM, ANSP, Boston University, Cornell University, Tula University, Zoological Museum of Copenhagen, and the Bureau Commercial Fisheries Biological Laboratory, Brunswick, Georg Specimens of *balao* and *brasiliensis* from the eastern Atlantic as w as from the western Atlantic were studied.

Discussion.—Juveniles of *Hemiramphus balao* and *H. brasiliensis* pelagic and are carried by the Gulf Stream north of the normal ran of the adults. Juveniles of *balao* have been taken at Bermuda, but specimens of *brasiliensis* have been found within a few hundred mi of Bermuda. It seems most reasonable to assume that *bermuden* differentiated from individuals of *brasiliensis* that drifted to Bermu in some past time. Juveniles of *brasiliensis* may still reach Bermu but if so, presumably they are unable to survive or reproduce competition with the very abundant *bermudensis.*

Because both *Hemiramphus balao* and *H. brasiliensis* show lit differentiation over their entire range, which covers both the east and western Atlantic, it was quite unexpected to find that the B mudan derivative of *H. brasiliensis* had differentiated to the spec level. It would have seemed more reasonable for the Bermuda pop lation of *Hyporhamphus* to become differentiated to the specific le for there are a large number of slightly differentiated populations *H. unifasciatus* throughout its range. The Bermudian population *Hyporhamphus* is only slightly different from other populations the species.

Endemism in Bermudian Shore Fishes

The presence in Bermuda of an endemic halfbeak apparently rived from the otherwise wide-ranging *Hemiramphus brasiliensis* lea to the question of how widespread endemism is in the other sh fishes of Bermuda. With this in mind a survey of other fishes thou to be endemic to these islands was made. Bermuda is an ocea island whose shore fishes have plainly been derived primarily fr the West Indies by way of the Gulf Stream system (Tee-Van, 19 Beebe and Tee-Van, 1933b). It would seem that a continued infl of individuals via the Gulf Stream would tend to make endemi rather rare. This is borne out by the survey which shows that of approximately 70 forms of shore fishes originally described as n

species or subspecies from Bermuda, 13 appear to be valid endemics. The 13 represent less than 4 per cent of the total Bermudian shore fish fauna. Table 4 lists, in phylogenetic order, the species that were originally described from Bermuda and their subsequent history. In addition to the apparently valid endemics, there are a number of species, known only from their original descriptions, or from very few subsequent records, the status of which can best be considered as uncertain. Eleven of the endemics can be considered as true shore fishes: *Branchiostoma bermudae, Harengula callolepis, Jenkinsia viridis, Engraulis choerostomus, Paraconger harringtonensis, Hemiramphus bermudensis, Fundulus heteroclitus bermudae, Allanetta harringtonensis harringtonensis, Haemulon aurolineatum angustum, Eupomacentrus chrysus* and *Lythrypnus mowbrayi*. The endemic seahorse, *Hippocampus hudsonius kincaidi,* and the pipefish, *Syngnathus mackayi nesiotes,* are in a somewhat different category because their West Indian ancestors are common elements of the sargassum weed fauna, and there is a greater possibility of their drifting onto the shores of the islands (Tee-Van, 1930), thus preventing complete isolation.

It is of interest to note that three of the endemic species have more gill-rakers than the species from which they apparently have been derived: *Harengula callolepis* has more than *H. humeralis* (Rivas, 1950); *Jenkinsia viridis* has more than *J. lamprotaenia* (Rivas, 1946 and Collette, in press); and *Hemiramphus bermudensis* has more than *H. brasiliensis*. Specimens of *Opisthonema oglinum* from Bermuda, the West Indies and Panama have a higher mean number of gill-rakers than those from the remainder of the mainland (F. H. Berry, personal communication). At least three of the endemics (*Harengula callolepis, Hemiramphus bermudensis* and *Haemulon aurolineatum angustum*) have a lesser body depth and the first two of these reach a greater length than do the species from which they have been derived. These characters may all be correlated with the scarcity of food caused by the general low level of nutrients in the Sargasso Sea around Bermuda (see Menzel and Ryther, 1960, 1961 and included references).

TABLE 4

SPECIES DESCRIBED FROM BERMUDA AND THEIR SUBSEQUENT HISTORY. (** = ENDEMIC SPECIES; * = ENDEMIC SUBSPECIES; ? = DOUBTFULLY ENDEMIC FORM; ALL OTHERS CONSIDERED NON-ENDEMIC.)

Family	Species and describer	Subsequent history
1. Branchiostomidae	**1. *Branchiostoma bermudae* Hubbs, 1922	Bermuda endemic, Bigelow & Farfante, 1948:11
2. Clupeidae	2. *Sardinella pinnula* Bean, 1912	= *S. anchovia* Cuv. & Val., Beebe & Tee-Van, 1933a:135
	**3. *Stolephorus viridis* Bean, 1912	= *Jenkinsia viridis,* Collette, in press
	4. *Jenkinsia bermudana* Rivas, 1946	= *J. viridis* (Bean), Collette, in press
	**5. *Harengula callolepis* Goode, in Goode & Bean, 1879	Bermuda endemic, Rivas, 1950:285
3. Engraulidae	**6. *Engraulis choerostomus* Goode, 1874	= *Anchoa choerostoma,* Bermuda endemic, Panama & Puerto Rico records referrable to other species, Hildebrand, 1943:71
4. Muraenidae	?7. *Gymnothorax brunneus* Nichols, 1920	Possibly = *Enchelycore nigricans* (Bonnaterre), a West Indian species, J. E. Böhlke (personal communication)
	?8. *Muraena aurea* Mowbray, 1931	Known only from 3 specimens, Beebe & Tee-Van, 1933b:53
5. Congridae	**9. *Leptocephalus harringtonensis* Mowbray, 1931	= *Paraconger harringtonensis,* a Bermuda endemic, Kanazawa, 1961:12
6. Ophichthidae	10. *Callechelys bilinearis* Kanazawa, 1952	+ Bahamas, J. E. Böhlke (personal communication)
	?11. *Quassiremus goslingi* Beebe & Tee-Van, 1932	Known only from 3 types, Beebe & Tee-Van, 1933b: 44
7. Belonidae	12. *Belone Jonesii* Goode, 1877	= *Tylosurus acus* (Lacépède), Jordan & Fordice, 1887: 355; Berry & Rivas, 1962

TABLE 4 (Continued)

Family	Species and describer	Subsequent history
8. Hemiramphidae	**14. *Hemiramphus bermudensis* Collette, 1962	See text
9. Exocoetidae	15. *Exonautes nonsuchae* Beebe & Tee-Van, 1932	= *H. hudsonius kincaidi* Townsend & Barbour, Ginsburg,
10. Syngnathidae	16. *Hippocampus brunneus* Bean, 1906	= *H. hudsonius kincaidi* Townsend & Barbour, Ginsburg, 1937:568
	*17. *Hippocampus kincaidi* Townsend & Barbour, 1906	= *H. hudsonius kincaidi,* Ginsburg, 1937:568
	18. *Corythoichthys bermudensis* Beebe & Tee-Van, 1932	= *Syngnathus dunckeri* Metzelaar, Longley & Hildebrand, 1941:59; Herald, 1942:131
	19. *Siphostoma dendriticum* Barbour, 1905	= *Amphelikturus dendriticus* + Bahamas, Herald, 1942: 132
	20. *Syngnathus Jonesii* Günther, 1874	= *Micrognathus vittatus* (Kaup), Herald, 1942:131
	*21. *Syngnathus mackayi nesiotes* Herald, 1942	Dwarf form
	22. *Syngnathus pipulus* Beebe & Tee-Van, 1932	= *S. elucens* Poey, Herald, 1942:131
11. Cyprinodontidae	*23. *Fundulus Bermudae* Günther, 1874	= *F. heteroclitus bermudae,* Hubbs, 1926:8; Miller, 1955:3
	24. *Fundulus rhizophorae* Goode, 1877	= *F. heteroclitus bermudae,* by implication, Hubbs, 1926: 8; listed, Jordan, Evermann & Clark, 1930:175
12. Holocentridae	25. *Holocentrus meeki* Bean, 1906	= *H. rufus* (Walbaum), Woods, 1955:104
	26. *Holocentrus puncticulatus* Barbour, 1905	= *H. coruscus* Poey, Rosen, 1911:53; Longley, 1932:299; Longley & Hildebrand, 1941:54; Woods, 1955:112

TABLE 4 (Continued)

Family	Species and describer	Subsequent history
13. Atherinidae	*27. *Atherina Harringtonensis* Goode, 1877	= *Allanetta harringtonensis* and represented in Florida, Puerto Rico and Panama by *A. h. araea* (Jordan & Gilbert), Jordan & Hubbs, 1919:38
14. Serranidae	?28. *Anthias louisi* Bean, 1912	Known only from type and 1 questionable specimen, Beebe & Tee-Van, 1933b:138; 4 additional specimens at Chicago (CNHM 4882) L. P. Woods (personal communication)
	?29. *Anthias tenuis* Nichols, 1920	Known only from type and 1 specimen from a fish stomach, Beebe & Tee-Van, 1933b:138; CNHM 48498 may be additional material, L. P. Woods (personal communication)
	30. *Liopropoma mowbrayi* Woods & Kanazawa, 1951	= *Chorististium mowbrayi,* + Bahamas, Starck & Courtenay, 1962:162
15. Scombropidae	?31. *Parasphyraenops atrimanus* Bean, 1912	Known from stomachs of fishes taken at 250 feet, Bermuda, Beebe & Tee-Van, 1933b:118
16. Lutjanidae	?32. *Neomaenis hastingsi* Bean, 1898	= *Lutjanus hastingsi;* may be only a variant of *L. vivanus* (Cuv. & Val.), Beebe & Tee-Van, 1933b:148
17. Pomadasyidae	*33. *Bathystoma aurolineatum angustum* Ginsburg, 1948	Described in a review of Western Atlantic *Bathystoma,* Ginsburg, 1948:155; placed in *Haemulon,* Courtenay, 1961:118
18. Gerridae	34. *Diapterus Lefroyi* Goode, 1874	= *Eucinostomus lefroyi,* + Cuba, Goode, 1876:41; + Florida, Puerto Rico, Cuba, Evermann & Marsh, 1902:207; + Bahamas, Rosen, 1911:57
	35. *Eucinostomus mowbrayi* Beebe & Tee-Van, 1932	= *E. havana* (Nichols), Longley & Hildebrand, 1941:140
	36. *Gerres Jonesii* Günther, 1879	= *Eucinostomus argenteus* Baird & Girard, Longley & Hildebrand, 1941:139
19. Chaetodontidae	37. *Centropyge argi* Woods & Kanazawa, 1951	+ Campeche Banks, north of Yucatan, Woods, 1952:269; + Curacao, Virgin Is., J. E. Randall (personal communi-

TABLE 4 (Continued)

Family	Species and describer	Subsequent history
	38. *Holacanthus ciliaris Bermudensis* Goode, 1876	= *H. bermudensis*, which has priority over *Angelichthys isabelita* Jordan & Rutter in Jordan & Evermann, 1898, from Florida, Beebe & Tee-Van, 1933a:149
20. Pomacentridae	39. *Chromis bermudae* Nichols, 1920	= *C. enchrysurus* (Jordan & Gilbert), L. P. Woods (personal communication)
	**40. *Eupomacentrus chrysus* Bean, 1906	= *E. chrysus*, a valid endemic, L. P. Woods (personal communication). Does not = *E. planifrons* Cuv. & Val. as suggested by Rivas, 1960:144
21. Labridae	41. *Bermudichthys subfurcatus* Nichols, 1920	= *Thalassoma bifasciatum* (Bloch), Longley, 1932:300; Beebe & Tee-Van, 1933a:151; Longley & Hildebrand, 1941:196
	42. *Iridio bathyphilus* Beebe & Tee-Van, 1932	+ Gulf of Mexico, J. E. Böhlke (personal communication)
	43. *Iridio decoratus* Bean, 1906	= *Halichoeres garnoti* (Cuv. & Val.), Longley, 1932:300; Beebe & Tee-Van, 1933a:151; Longley & Hildebrand, 1941:193
	44. *Iridio elegans* Bean, 1906	= *Halichoeres radiata* (Linnaeus), Mowbray, 1931; Longley, 1932:300; Beebe & Tee-Van, 1933a:150; Longley & Hildebrand, 1941:192
	45. *Iridio frenatus* Nichols, 1920	= *Halichoeres maculipinna* (Muller & Troschel), Longley, 1932:300; Beebe & Tee-Van, 1933a:150; Longley & Hildebrand, 1941:190
	46. *Iridio meyeri* Bean, 1906	" "
	47. *Iridio microstomus* Bean, 1906	" "
	48. *Iridio similis* Nichols, 1920	" "
	49. *Julis nitidissima* Goode, 1877	= *Thalassoma bifasciatum* (Bloch), Beebe & Tee-Van, 1933a:151; Longley & Hildebrand, 1941:196

TABLE 4 (Continued)

Family	Species and describer	Subsequent history
22. Scaridae	50. *Cryptotomus crassiceps* Bean, 1906	= *C. roseus* Cope, Longley, 1932:300; Beebe & Tee-Van, 1933a:152; Longley & Hildebrand, 1941:205; Schultz, 1958:127
	51. *Pseudoscarus plumbeus* Bean, 1912	= *Scarus coelestinus* Cuv. & Val., Longley, 1932:300; Longley & Hildebrand, 1941:221; Schultz, 1958:105
23. Blenniidae	52. *Emblemaria marki* Mowbray & Bean, 1912	= *E. atlantica* Jordan & Evermann, Böhlke, 1957:49
	53. *Hypleurochilus bermudensis* Beebe & Tee-Van, 1933	+ Tortugas, Longley & Hildebrand, 1941:268
24. Clinidae	54. *Labrisomus lentiginosus* Bean, 1906	= *L. nuchipinnis* (Quoy & Gaimard), Longley, 1932:300; Longley & Hildebrand, 1941:250; Springer, 1959a:427
	55. *Somersia furcata* Beebe & Tee-Van, 1934	= *L. nuchipinnis* (Quoy & Gaimard), Springer, 1959b:291
25. Microdesmidae	56. *Microdesmus woodsi* Kanazawa, 1952	=*M. longipinnis* (Weymouth), Robins & Manning, 1958:301
26. Brotulidae	57. *Brosmophycis Verrillii* Garman, 1900	= *Dinematichthys cayorum* (Evermann & Kendall), Longley & Hildebrand, 1941:277
	58. *Grammonus mowbrayi* Grey, 1951	+ Bahamas, J. E. Böhlke (personal communication)
27. Ophidiidae	59. *Otophidium schmidti* Woods & Kanazawa, 1951	= *Parophidion schmidti,* + Bahamas, Böhlke & Robins, 1959:51; + Jamaica, Robins & Böhlke, 1959:9
28. Carapidae	60. *Lefroyia Bermudensis* Jones, 1874	+ Puerto Rico, Evermann & Marsh, 1902:319; + Tortugas, Longley & Hildebrand, 1941:282; = *Carapus bermudensis,* + Florida & West Indies, Arnold,

TABLE 4 (Continued)

Family	Species and describer	Subsequent history
29. Callionymidae	61. *Callionymus bermudarum* Barbour, 1905	= *C. dubiosus* Parr from Bahamas, synonymous with *C. bermudarum,* Beebe & Tee-Van, 1933a:155
30. Acanthuridae	62. *Teuthis helioides* Barbour, 1905	= *Acanthurus coeruleus* Bloch & Schneider, Longley, 1932:300; Longley & Hildebrand, 1941:155; Randall, 1956:222
31. Gobiidae	**63. *Rhinogobius mowbrayi* Bean, 1906	= *Lythrypnus mowbrayi,* a valid Bermuda endemic closely related to *L. crocodilus* (Beebe & Tee-Van) from Haiti, Böhlke & Robins, 1960:81
32. Scorpaenidae	64. *Pontinus microlepis* Bean, 1912	= *P. castor* Poey, Ginsburg, 1953:49
33. Icosteidae	?65. *Eucrotus ventralis* Bean, 1912	Listed only from Bermuda, Jordan, Evermann & Clark, 1930:267
34. Monocanthidae	66. *Monacanthus tuckeri* Bean, 1906	+ Puerto Rico, Nichols, 1915:145; + Tortugas, Longley & Hildebrand, 1941:297; + Carolinas, Florida, Bahamas, Lesser Antilles, Berry & Voegle, 1961:69
35. Ostraciidae	?67. *Lactophrys saxatilis* Mowbray, 1931	Known only from 2 types, Beebe & Tee-Van, 1933b:244
36. Antennariidae	68. *Antennarius bermudensis* Schultz, 1957	+ Bahamas, J. E. Böhlke (personal communication)
	69. *Antennarius stellifer* Barbour, 1905	= *A. multiocellatus* (Cuv. & Val.), Barbour, 1942:27; Schultz, 1957:94
	70. *Antennarius verrucosus* Bean, 1906	+ Florida, Schultz, 1957:99
	71. *Histrio jagua* Nichols, 1920	= *H. histrio* (Linnaeus), Barbour, 1942:24; Schultz, 1957:104

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THE AMERICAN PERCID FISHES OF THE SUBGENUS *VILLORA*

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I. Introduction

The aims of this paper are threefold: to define the subgenus *Villora,* to resurrect and define *Etheostoma (Villora) okaloosae* (Fowler), and to examine intra-specific variation in *E. (Villora) edwini. Villora* was described as a new genus by Hubbs and Cannon (1935) on the basis of the new species *edwini.* Bailey (1951), in Bailey Winn and Smith (1954), and in Bailey and Gosline (1955) reduced the many nominal genera of darters to three: *Percina, Ammocrypta* and *Etheostoma.* In 1955 (Fig. 1), Bailey and Gosline arranged the darters in order of increasing specialization and some former genera were utilized as subgenera. *Etheostoma edwini* was listed under the subgenus *Hololepis,* without further comment. We cannot subscribe to this view. During his study of the subgenus *Hololepis,* the senior author (Collette, 1960) became convinced that *Villora* should be regarded as distinct from *Hololepis.* Through extensive collecting in western Florida, the junior author (Yerger, 1960) discovered that *Etheostoma okaloosae* (Fowler) is a valid species referable to the subgenus *Villora,* and concluded that it must be removed from the synonymy of *E. swaini* (Jordan) where it was placed by Bailey, Winn and Smith (1955).

The methods of this study are similar to those of Collette (1962). However, here we present the counts of the unpored (Table 3) as well as the pored and total lateral-line scales. This character is unimportant in the subgenus *Hololepis,* but proves most useful in *Villora.* Measurements were made following the technique described by Hubbs and Cannon (1935). In the course of this study, more than 1100 specimens of *E. edwini* and nearly 200 of *E. okaloosae* were examined. For purposes of comparison, summary counts for the two species of *Villora* are being presented along with those for the species of *Hololepis* in another paper (Collette, 1962, Tables 38-49).

II. Acknowledgments

The section on *Etheostoma edwini* is based on part of a doctoral dissertation presented to Cornell University by the senior author. Professor Edward C. Raney, who served as chairman of the committee, provided, in addition to constant interest, support for the study through National Science Foundation Grants 2893 and 9038.

The section on *E. okaloosae* is part of a study on the fishes of the Florida panhandle undertaken by the junior author with support from a National Science Foundation Grant G-6260 and from the Research Council of the Florida State University. The many contributions to this project by Ardith B. Cochran are gratefully acknowledged, as are the services rendered by W. Bruce Walden and Robert F. Christensen, graduate students at Florida State University. Colonel John N. Reynolds, Commander, Eglin Air Force Base, Florida, granted permission to collect on the military reservation and extended many courtesies. James E. Böhlke compared the type of *E. okaloosae* with several specimens sent to him by the junior author.

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III. Subgenus *Villora*

Villora Hubbs and Cannon, 1935:11-13 (type species *Villora edwini* Hubbs and Cannon, 1935, by original designation).

Lateral line slightly arched upward, incomplete to complete; pored lateral-line scales 20 to 36, unpored 0 to 18, total 32 to 42; infraorbital canal always complete, usually with 8 pores; supratemporal canal usually complete in adults; coronal pore present; interorbital pores usually 2; preoperculomandibular pores usually 9 or 10; vomer and palatine toothed; preopercle entire or crenulate; branchiostegal membranes separate or narrowly conjoined; branchiostegal rays usually 6; breast naked to entirely covered with scales; nape, preopercle, and opercle completely covered with imbedded cycloid to exposed ctenoid scales; parietal and interorbital regions naked; belly covered with unmodified ctenoid scales; flesh opaque; body rather stocky and somewhat compressed; vertebrae 33 to 38; premaxillary frenum broad; first dorsal fin moderately high, with 8 to 11 spines that lack thickened fleshy tips; second dorsal fin somewhat higher than first dorsal, with 9 to 13 rays; anal spines usually 2, the first thicker than the second; anal soft-rays 5 to 9; pectoral rays usually 12 or 13; segmented caudal rays: upper 8 to 13, lower 7 to 10, total 15 to 22; genital papilla of breeding female a low tube crowned with villi; pelvic fins closely approximated, separated by a distance equal to about one-half the pelvic base; dark humeral spot behind the opercle and above the pectoral fin origin usually prominent; breeding tubercles absent; males reaching a larger maximum size than females; habitat moderately fast, clear streams with patches of vegetation; range northern and western Florida and below the Fall Line in southwestern Georgia and in Alabama.

Hubbs and Cannon (1935) placed *Villora* between *Hololepis* and the catch-all *Poecilichthys*. They felt that many of the features of *Villora* were primitive and suggested that it may have evolved from an ancestor of *Hololepis*. The relationships of *Villora*, however, do not seem to lie with *Hololepis* (see Collette, 1962). The rediscovery of *E. okaloosae*, which is obviously closely related to *E. edwini* and more different from *Hololepis* than *edwini*, gives support to our view that *Villora* should stand as a subgenus separate from *Hololepis*. In a number of characters *E. okaloosae* is somewhat intermediate between *E. edwini* and E. *(Oligocephalus) swaini* (Jordan). There seems to be a trend toward a shorter genital papilla (Fig. 7), a more highly arched lateral line, a slenderer caudal peduncle, and fewer pored lateral-line scales as one moves from *E. (O.) swaini* through *E. (V.) okaloosae* to *E. (V.) edwini*. In the last three characters the evolutionary trend parallels that of the subgenus *Hololepis*, resulting in a superficial similarity between the *Villora* and *Hololepis* lines. *Villora* differs from the subgenus *Hololepis* by lacking breeding tubercles and by having a nearly complete lateral line, extending past the origin of the second dorsal fin (occasionally complete in *E. okaloosae*); a much less arched lateral line; the genital papilla in the form of a low tube crowned with villi (Collette, 1962: Fig. 1); and a dark humeral spot. The species live in clear, moderately fast-flowing, sandy-bottomed streams. *Villora* differs from many of the species of the subgenus *Oligocephalus* in having a somewhat arched lateral line and in the shape of the genital papilla. We have not studied thoroughly the differences between *Oligocephalus* and *Villora*. This matter deserves further study.

IV. Species of *Villora*

The two species that we refer to the subgenus *Villora* differ in a number of respects (Table 1). Frequency distributions of the more important characters are presented in

Tables 2-8. Table 9 compares the proportional measurements of the two species.

Etheostoma (Villora) edwini
(Hubbs and Cannon)

Villora edwini—Hubbs and Cannon, 1935:13-16 (original description); Carr, 1937:83 (Fla.); Fowler, 1941:242, fig. 13 (not 3 as given) (Fla.); Bailey and Hubbs, 1949:10 (*edwini* one of a group of endemic species, probably relicts, in sinkhole region of N. Fla.).

Etheostoma edwini—Bailey, Winn, and Smith, 1954:144, 156 (range extension W to Perdido R., and N into S Ala.); Bailey and Gosline, 1955:20, 43-44 (number of vertebrae); Carr and Goin, 1955: 31, 101-102, pl. 30 (description, Fla.); Eddy, 1957: 220, 223, fig. 552; Moore, 1957:197; Neill, 1957:196 (distribution in Fla. stops at the Suwannee Straits, although habitat continues); Briggs, 1958: 275 (distribution); Crittenden, 1958:218 (Bay Co., Fla.); Yerger, 1960:41 (comparison with *E. okaloosae*); Collette, 1961: 1051.

Fowler's reports (1945: 251-252, 293-294) of *Villora edwini* from Ware County, Georgia and from Florida were based on *E. fusiforme barratti.*

Types—Holotype UMMZ 87892; 38 mm male; Fla., Santa Fe R., at Poe Springs; Feb. 8, 1928; E. T. Boardman. Paratypes, the rest of the specimens examined by Hubbs and Cannon (1935:13).

Coloration—The first dorsal fin of the female varies from almost clear to having four rows of rectangular blotches on each interspinous membrane. The second dorsal fin is colored like the first dorsal but has additional pigment on the rays, producing a barred appearance. Melanophores usually outline the anal and pectoral rays; the anal membranes are clear or have a few pigment cells. The pelvic fin is clear, with occasional melanophores on the rays. The caudal rays are barred; the membranes sometimes have pigment. Both belly and breast vary from being immaculate to having scattered large melanophores. The cheek has small and medium melanophores. All four orbital bars are developed; the suborbital is the most prominent; the supraorbital and suborbital both enter the eye. The pored portion of the lateral line is light, with pigment underneath some scales. Most specimens lack distinct basi-caudal spots; some have blackish median spots and vestiges of dorsal and ventral spots. Eight to twelve lateral blotches are sometimes present along the sides; they may extend down to the underside of the caudal peduncle. There are usually about nine dark brown dorsal saddles. Melanophores on the sides below the lateral line are generally arranged in a prominent X-pattern as described by Hubbs and Cannon (1935). Chromatophores below the lateral line are mostly black; those above the lateral line are brown. The genital papilla is usually devoid of pigment, but the dorsal surface of the distal portion is sometimes pigmented. Figure 1 shows the pattern of a breeding female.

In the non-breeding male the pectoral and caudal fins, orbital bars, basi-caudal spots and sides of the body are colored as in the female. The first dorsal fin is similar to but darker than that of the female. Small melanophores occur between the blotches on the second dorsal fin. The proximal three-fourths of the anal fin and and the proximal seven-eighths of the pelvic fin membranes are covered with small melanophores. Both belly and breast are covered almost entirely with small melanophores. The cheek is darker than that of the female. The light, pored portion of the lateral line stands out more sharply against the dark sides of the male. The lateral blotches and the dorsal saddles are usually more prominent in the male. The genital papilla is free from pigmentation and there is no pigment on the belly dorsal to it.

The basi-caudal spots, orbital bars, cheek and genital papilla of the breeding male are colored as in the non-breeding male. The blotches in the dorsal fins have orange centers. Most breeding males have three or four rows of such spots on the membranes of the first dorsal fin and three to five rows on the membranes of the soft-dorsal. Black pigment is concentrated anterior and posterior to the last dorsal spine. The anal fin also has orange spots which are usually arranged in one or two rows, and the entire fin is darkened by melanophores. The pelvic fin is covered with small melanophores. The pectoral fin differs from that of the species of the subgenus *Hololepis* in having at least the basal half of its membranes covered with small melanophores. In addition to the barring of the caudal rays there are small mel-

Figures 1-3. Females of three species of *Etheostoma*. 1. (Upper) *E. edwini*, FSU 6178 Mar. 25, 1960, 35.4 mm. 2. (Middle) *E. okaloosae*, FSU 6078, Jan. 25, 1960, 40.0 mm 3. (Lower) *E. swaini*, FSU 1632, Mar. 5, 1954, 35.8 mm.

anophores on the interradial membranes. The belly, breast and branchiostegal membranes are uniformly sprinkled with small melanophores. The narrow light streak along the lateral line is not prominent. There are light (orange in life) spots on the sides, both above and below the lateral line. The dorsal saddles are sometimes indistinct. Figure 4 shows the pigment pattern of a breeding male compared with males of *E. okaloosae* and *E. swaini*.

Fowler (1941) presented a drawing labeled as *Villora edwini* (Fig. 3), and another labeled as *Hololepis barratti* (Fig. 13). The labels on these drawings were apparently reversed, since the scale on Figure 3 indicates a fish of about 26 mm total length (close to the stated length of the specimen of *barratti*, 29 mm) and that on Figure 13 indicates a fish of about 41 mm (close to the stated length of the specimen of *edwini*, 44 mm). Figure 13 is clearly intended to represent *Villora edwini* since the pored portion of the lateral line extends behind the end of the second dorsal fin and there are no prominent basi-caudal spots. The pored portion of the lateral line in Figure 3 extends only to the end of the first dorsal fin, and there are three prominent basi-caudal spots, characters indicative of *barratti*. However, there are too few lateral-line scales in the figure to portray *Etheostoma fusiforme barratti* accurately.

The colors of *E. edwini* in life are very striking, and the presently accepted common name, brown darter, does not portray adequately the distinctive characters of this species. A more descriptive common name is redspot darter. The following descriptions are based on a composite of field notes (by Yerger) on series collected from January through April. Males in full breeding color have orange-red spots scattered over the body from the back of the oper-

Figures 4-6. Males of three species of *Etheostoma*. **4.** (Upper) *E. edwini*, FSU 6154, Mar. 26, 1960, 36.8 mm. **5.** (Middle) *E. okaloosae*, FSU 6078, Jan. 25, 1960, 43.4 mm. **6.** (Lower) *E. swaini*, FSU 6071, Jan. 23, 1960, 39.6 mm.

culum to the caudal fin, above the lateral line, and extending halfway from the lateral line to the ventral contour of the body. The largest spots, about the size of the pupil, are immediately above and below the lateral line. Each spot consists of a central red portion surrounded by a yellow ring. The spinous dorsal fin has a prominent basal row and a sub-marginal row of orange-red spots, with two irregular rows between them. A large black blotch is present on the posterior part of the membrane, centered between the last two spines. The second dorsal fin has four similar rows of slightly smaller orange-red spots, and lacks the black area. There are two incomplete rows of reddish spots on the anal fin, best developed on the posterior third of the membrane. The caudal has three to six vertical bands of elongate reddish or reddish-brown blotches, most prominent on the base of the fin. The pelvics are dusky. The general body color is tan to yellow brown, with irregular darker blotches below the lateral line. Males with less brilliant coloration and younger males are generally more yellow and possess fewer spots on the body and on the dorsal and anal fins. Neither *E. okaloosae* nor any species of the subgenus *Hololepis* has red spots on the body.

Females lack the brilliant orange-red spots on the fins, but have several rows of very small reddish spots just above and parallel

to the lateral line. The caudal fin is like that of the male, but has smaller and more numerous reddish to yellowish spots. The pelvics are clear. The black coloration below the lateral line contrasts more strikingly with the tan coloration above the lateral line than in the males.

Genital Papilla — Hubbs and Cannon (1935:14) described the genital papilla of *E. edwini* as follows: "In the breeding female scarcely developed as such, represented by matted villi surrounding the oviducal opening; some villi long enough to reach anal fin; in the non-breeding female shrunken but preserving the villous appearance." Examination of a large number of specimens

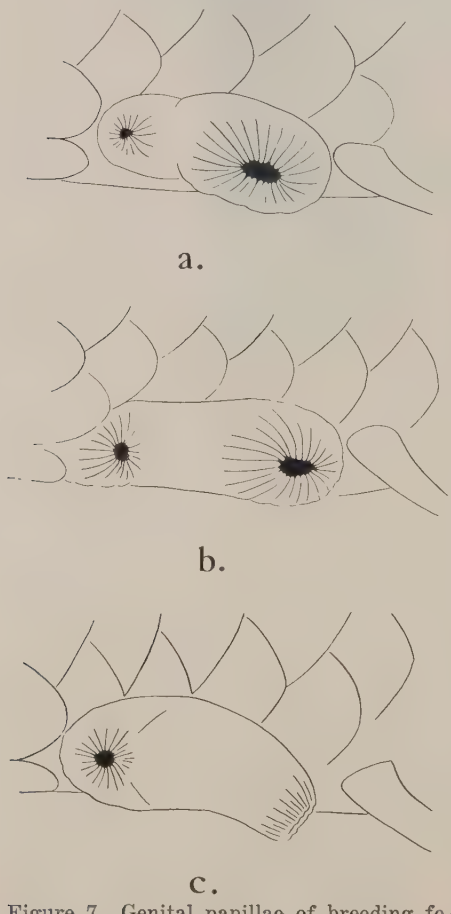

Figure 7. Genital papillae of breeding females of three species of *Etheostoma*. **a.** (Upper) *E. edwini*. **b.** (Middle) *E. okaloosae*. **c.** (Lower) *E. swaini*.

indicates the need for modifying this de scription. The papilla of the breeding fe male is a short tube, containing rugae whic form villi at the terminus of the papill The thin membrane connecting these ruga tends to break from excessive probing c from the use of an air jet; the ends of th rugae then appear as free villi. Figure 7 shows the genital papilla of a typical fe male in breeding condition.

Development — Little information i available on the development of *E. edwin* One collection (UF 6962) from th Apalachicola River system contains speci mens as small as 11 mm SL. Plotting pore lateral-line scales against standard lengt for this collection (Fig. 8) gives abou the same picture for their development a found in *E. fusiforme fusiforme* (Collett 1962: Figs. 12 and 13). An 11.3 mm specimen lacked scales on the anterior por tion of the body while another, 11.0 mm long, had the body completely scaled. Th pored scales begin developing at about 12 13 mm. Figure 8 shows an intermediat group from about 15-21 mm which indi cates that the definitive number of pore lateral-line scales may not be formed unti a length of about 22 mm has been at tained.

The same collection furnishes data on th size at which the supratemporal canal be comes complete. Specimens from 36.6 mm to 21.7 mm long are about equally divide between those with the canal complete an those with the canal incomplete, but al from 21.7 to 11.0 mm long have incom plete canals. A 12.0 mm specimen ha only a shallow groove and completely lack a roofed-over supratemporal canal. Adult of *E. edwini* typically have this canal com plete, but individuals in a number of col lections retain the juvenile incomplete con dition.

Habitat — *E. edwini* usually lives i clear to slightly turbid streams varying i depth from six inches to two or three feet The current is usually moderate. The bot tom consists chiefly of sand with an oc casional light overlay of fine silt, or som gravel, and occasionally rock outcrops. Th vegetation varies from sparse to dense. Th list of plants is long, and varies to som extent from one locality to another, but fre quently consists of species of *Ludwigia Scirpus, Orontium, Nitella,* and *Batracho*

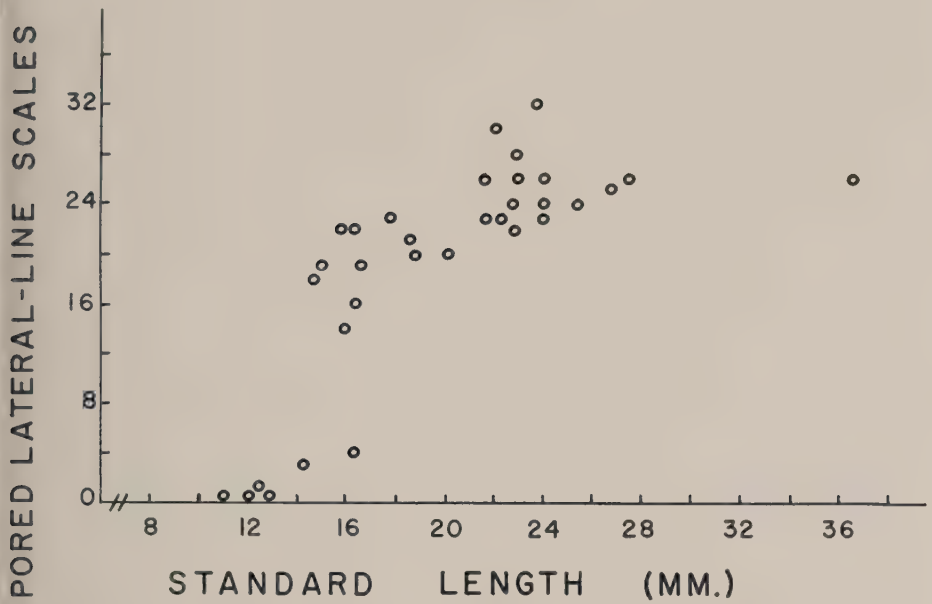

Figure 8. Change in number of pored lateral-line scales with size in *Etheostoma edwini*. (UF 6962, Fla., Apalachicola Dr., Dec. 2, 1939).

spermum. The pH varies from 6.4 to 7.8, the more alkaline readings having been recorded in spring runs with limestone outcrops.

Both species of the subgenus *Villora* prefer faster, clearer and more alkaline situations than do the species of the sugenus *Hololepis*. Crittenden (1958) gave some of the physical and chemical characters of two streams in Bay Co., Fla., one of which is inhabited by *Etheostoma edwini* and the other by *Etheostoma (Hololepis) fusiforme barratti*. The stream with *E. edwini* — Econfina Creek—"is spring-fed, clear, fast-flowing fresh water creek over most of its course; depths are three to ten feet near the mouth; and the bottom is of sand and limestone in its upper reaches." The pH was 7.5-7.8 and the methyl orange alkalinity was 45.5-56.0 p.p.m. The stream containing *E. f. barratti*—Cedar Creek—"is a sluggish slow-moving stream with currents noticeable only at low tide; the sand and mud bottom had a vegetable detritus overlay; depths vary from three to ten feet and the water is stained." The pH was 7.3 and the methyl orange alkalinity 35.0 p.p.m.

Habits—These darters are most frequently found beneath the leaves of scattered clumps of vegetation toward the margins of the streams rather than in the main current. Nothing is known about their spawning behavior, but since the genital papilla and the ecological requirements of *E. edwini* are so similar to those of *E. okaloosae*, it is highly probable that in behavior the two species are very much alike.

Examination of the ovaries of females and the development of breeding color in males indicates that the breeding season is at its height in February, March, and early April. Ripe ova occasionally observed in specimens collected as late as June indicate that the spawning season may be prolonged. Specimens as small as 11.0 mm SL. (UF 6962, Chipola R., Florida) were collected by William MacLane on December 2 in dense clumps of filamentous algae. The presence of fry in the beginning of December indicates that some individuals may spawn in the fall, at least in some years. Since this river originates from springs, its ecological conditions may differ from those in neighboring streams.

The males of *E. edwini* are considerably larger than the females. The largest male examined is 48.8 mm long (FSU 3404, Ochlockonee R.) and the largest female

39.9 mm (FSU 2218, Apalachicola R.). In the subgenus *Hololepis* the females are larger or the sexes are of equal size. Males of *E. edwini* have much brighter colors than do the males of the species of *Hololepis*. These characters would seem to be of advantage only to territorial species. Winn (1958:172) stated that for the darters he studied: "The male is larger than the female in all the species studied that have a well-developed territory . . ." with the exception of two species in which sex recognition and territoriality are easily disrupted. Hubbs and Cooper (1936), Noble (1938) and Raney and Lachner (1943) have also noted correlations between territorial behavior and degree of sexual dimorphism in color, size, or structure in various groups of freshwater fishes.

Distribution—Etheostoma edwini is limited to the Coastal Plain from the St. Johns River in northeastern Florida, west to the Perdido River of western Florida and southern Alabama, and north into Georgia as far as the Fall Line (Fig. 9). It is replaced by its relative *E. okaloosae* in several small streams tributary to Choctawhatchee Bay (Fig. 10).

Neill (1957) listed *E. edwini* as one of a group of species that has not crossed the Suwannee Straits to penetrate peninsular Florida. However, since the range of *E. edwini* does extend into Marion and Putnam counties in the St. Johns drainage *edwini* should be added to Neill's list of species that barely penetrate the peninsula.

On the basis of present knowledge it is impossible to determine where or when *E. edwini* differentiated. Its wide range east to west and northward to the Fall Line would indicate that it probably was in existence before the Pleistocene. Periodic encroachments of the sea must have forced it to retreat toward the headwaters, where it survived only in those larger river systems along the Gulf Coast that were not completely inundated by salt water. As sea-level receded, it moved downstream to occupy all suitable habitats, and surrounded the restricted range of *E. okaloosae*. At the

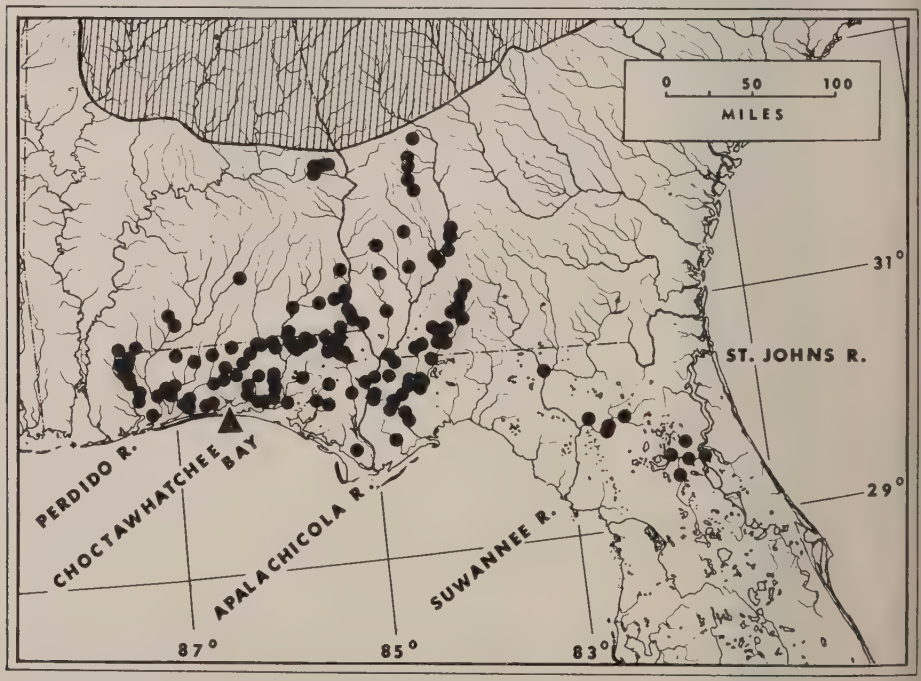

Figure 9. Distribution of *Etheostoma edwini* (dots) and of *E. okaloosae* (two streams at end of triangle) with reference to the Fall Line (taken from Fenneman, 1938 and 1946). (Based on specimens examined.)

present time, at several localities, streams occupied by *okaloosae* originate less than one mile from the headwaters of streams inhabited by *edwini,* but since the two species have never been taken together, there is no possibility of interbreeding under present conditions.

Geographic Variation — Since there is no appreciable variation in the number of pectoral rays (11-14, modes 13), condition of supratemporal canal (usually complete), number of interorbital pores (0-3, usually 2), or the squamation of the preopercle, opercle, and breast, summed frequency distributions have been presented in comparison with the data for *E. okaloosae* and the species of the subgenus *Hololepis* elsewhere (Collette, 1962: Tables 38-49).

The three easternmost populations (St. Johns, Suwannee, and Ochlockonee) have slightly more pored lateral-line scales ($\bar{x}$: 28.0, 29.9, 28.3) than the other populations ($\bar{x}$: 24.6 to 27.8) (Tables 2). This difference is correlated with the difference in number of total lateral-line scales. Populations in the St. Johns and Suwannee have higher means ($\bar{x}$: 38.1, 39.3); the westernmost population, the Perdido, also has a high mean (38.1); in the other populations the means vary from 37.1-37.6 (Table 4). The modal number of the scale rows above the lateral line is usually 3; the Suwannee and Ochlockonee populations have a mode of 4; the numbers are of about equal frequencies in the Flint system (Table 5). Most populations have a mode of 7 scale rows below the lateral line; the Suwannee population has a mode of 8; the westernmost populations, Pensacola Bay and Perdido drainage, have a mode of 6 (Table 5).

The modal number of first dorsal spines in most populations is 9 ($\bar{x}$:9.40 or less); the St. Johns and Suwannee populations again stand out with a modal number of 10 spines ($\bar{x}$: 9.69 and 9.55) (Table 6). The modal number of second dorsal rays is 11 in most populations; 10 in the Chipola and Choctawhatchee; 12 in the Chattahoochee population (Table 6). The modal number of anal soft-rays is 7 in all but two populations; the Chipola and Choctawhatchee populations have a mode of 6 rays (Table 8).

Most populations have modes of 10 preoperculomandibular pores but the three easternmost show a tendency toward fewer pores that is especially evident in the Ochlockonee population which has a mode of 9, thus resembling *E. okaloosae* (Table 7).

There is no evident geographic variation in extent of squamation except in the nape region. The eastern populations, through the Apalachicola, have the nape mostly I/PX-C/T to PX/X-T,* while the populations west of the Apalachicola (Choctawhatchee, Pensacola, Perdido) have modes of X/T (Table 8).

Three slightly differentiated races of *edwini* may be distinguished: (1) an eastern race (St. Johns and Suwannee) with more pored lateral-line scales, more total lateral-line scales, and more dorsal spines; (2) an Ochlockonee race with a modal number of nine preoperculomandibular pores and a high number of pored lateral-line scales; and (3) a western race (Pensacola, Perdido, Choctawhatchee) having more scales on the nape. The Apalachicola River is inhabited by a population lacking any differentiating characters. If other characters are used, these races may be further subdivided. The Suwannee population has on the average more scale rows above and below the lateral line than does the St. Johns population. The Choctawhatchee population has fewer dorsal and anal soft-rays, and more scale rows below the lateral line than do the Pensacola and Perdido populations. Even the Apalachicola populations can be subdivided: the Chipola population has more total lateral-line scales and fewer second dorsal rays; the Chattahoochee population has more second dorsal rays; the Flint population has an intermediate number of second dorsal rays.

Specimens Examined—Full locality data are given only for collections from the St. Johns River (range extension) and for the type locality. For the other collections, drainage, state, county, and museum number are listed. Complete data for most of the collections are contained in Collette (1960).

St. Johns Drainage, Fla.—Marion Co.: UF 6963 (6 specimens, 32-43 mm. in standard length), small spring cr., 5¾ mi. NE Bruceville on Salt Springs Rd., Oct. 13, 1948. Oklawaha R. at Davenport Landing, 6-7 mi. upstream from mouth: UF 6968 (22, 22-38), Mar. 26, 1949; UF 6966 (7, 25-27), Oct. 2, 1949; and UF 6967 (2, 27-28),

* Squamation designation follows Collette, 1962. I, PX, X refer to the relative imbedding of the scales (imbedded, partially exposed, exposed respectively); C and T stand for cycloid and ctenoid.

Oct. 7, 1949. CU 35138 (1), Oklawaha R. just E of Eureka on Fla. 316, Mar. 27, 1960. Putnam Co.: Acosta Cr., 1.5 mi. N Welaka on Fla. 309; UF 6969 (4, 33-39), Dec. 28, 1946; and UF 6970 (1, 34), Mar. 24, 1947. UF 1911 (11, 25-37), 9 mi. W Palatka on Keystone Heights Rd., Mar. 24, 1947. UF 99 (1, 38), Little Orange Cr., 6 mi. S Johnson, May 22, 1947.

Suwannee Drainage, 131 specimens. Fla. — Alachua Co.: Santa Fe R. at Poe Springs, type locality: USNM 94684 (1, 33) and UF 2674 (2, 32-33), Feb. 8, 1928, paratypes; UF 209 (2, 33-38), Mar. 19, 1934; CU 10198 (1, 34), Apr. 6, 1940; UF 2910 (5, 29-35), May 8, 1947; UF 52 (13, 24-35), Oct. 13, 1947; UF 6964 (35, 22-38), July 27, 1947; UF 298 (6, 22-36), July 15, 1952. Columbia Co.: ANSP 69160; UMMZ 166571; TU 8441; UF 2676, 8091, 8087, 8106, 8100, 8095, 8074, 8125, 8078, 8131, 8115, 8116, 8126, 8122, 8123, 8030. Gilchrist Co.: UF 6960, 8028. Hamilton Co.: UF 2675. Suwannee Co.: FSU 1742. Union Co.: UF 2677.

Ochlockonee Drainage, 125 specimens. Ga.—Colquitt Co.: CU 17768; FSU 4447, 4069. Decatur Co.: FSU 2979, 3011. Grady Co.: CU 29759; FSU 2885, 2863, 4201, 4191, 4489. Thomas Co.: FSU 3990, 3969. Fla.—Franklin Co.: FSU 4865. Gadsden Co.: UF 6959; FSU 1657, 1637, 2524, 2205, 3404, 4431. Leon Co.: UF 6935; FSU 654, 5174, 3927. Liberty Co.: UMMZ 158182; UF 6965; FSU 228, 166, 2797, 3754, 3872. Wakulla Co.: FSU 3851.

Apalachicola River

Flint-Apalachicola Drainage, 110 specimens. Ga.—Calhoun-Dougherty cos.: UMMZ 164083. Decatur Co.: UF 595, 4493; FSU 1736, 2218. Dougherty Co.: CU 17322; UMMZ 163969, 164033; BU uncat. coll.; Early Co.: CU 18235. Miller Co.: CU 23794. Randolph Co.: CU 17752. Schley Co.: CU 29751, 29754. Seminole Co.: UF 4560. Sumter Co.: CU 29757. Taylor Co.: CU 21147, 29750. Terrell Co.: CU 15795. Worth Co.: UMMZ 164013; BU 2 uncat. coll. Fla.—Gadsden Co.: FSU 4029, 6272.

Chattahoochee-Apalachicola Drainage, 34 specimens. Ga.—Early Co.: CU 29745; FSU 6627. Ala.—Henry Co.: CU 17487; TU 2560; FSU 6572. Houston Co.: TU 2542, 2338, 2325. Lee Co.: UMMZ 128786; CU 15995; FSU 6649. Russell Co.: API 551; CU 15600, 13977; TU 10716; FSU 6586, 6655.

Chipola-Apalachicola Drainage, 125 specimens. Ala.—Houston Co.: CU 17676, 17667; TU 2406; UAIC 381. Fla.—Calhoun Co.: FSU 3814. Jackson Co.: UMMZ 158204, 163469, 163478; UF 6936, 6962, 4896; CU 29749; TU 127, 2292, 2380; FSU 1698, 2826, 4090, 4174.

Other Apalachicola Drainage, 19 specimens. Fla.—Calhoun Co.: TU 2042. Gadsden Co.: UF 4916, 4941. Gulf Co.: FSU 3298. Liberty Co.: UF 6971, 6972.

St. Andrews Bay Drainage, 4 specimens. Fla.—Bay Co.: FSU 552, 5766; TU 21449.

Choctawhatchee Bay Drainage, 197 specimens. Fla.—Holmes Co.: UMMZ 163502; CU 12116; TU 183, 1091, 1598, 2283, 2485, 2461, 2304, 2309, 20409; UMMZ 166327; FSU 1702, 1619, 2805, 4129, 4408, 6309. Holmes-Jackson Cos.: FSU 4168. Okaloosa Co.: FSU 5165, 6048. Walton Co.: TU 1073, 310; CU 21773; TU 1694, 1610, 22750; FSU 368, 4154, 5378, 5411, 6026, 6178, 6125, 6154. Washington-Bay Cos.: TU 3643. Washington Co.: FSU 5053. Ala.—Dale Co.: TU 4037, 2520. Geneva Co.: TU 1703, 14286, 16383. Houston Co.: CU 29758; TU 2512.

Pensacola Bay Drainage, 249 specimens. Ala.—Conecuh Co.: UMMZ 155518. Crenshaw Co.: TU 14194. Escambia Co.: TU 14177; UAIC 417, 420. Fla.—Okaloosa Co.: UF 6961, 3359; UMMZ 166239; FSU 4732, 4744, 4996, 6094, 6183. Santa Rosa Co.: UF 1456; UMMZ 155506, 166220, 165134; TU 4590, 20535; UF 7879; FSU 4670, 4940, 4950. Walton Co.: UMMZ 166246, 166351; FSU 6060.

Perdido Drainage, 76 specimens, Ala.—Escambia Co.: CU 15603; TU 14183, 16366, 23978, 21188. Fla.—Escambia Co.: UMMZ 134605, 166173, 166188; FSU 2958, 4799, 4761, 4726, 5956, 5843, 5799, 5862, 5880.

Etheostoma (Villora) okaloosae (Fowler)

Villora okaloosae—Fowler, 1941:242, 244 (original description), fig. 12 (holotype); Fowler, 1945:40, 294 (reference to holotype).

Etheostoma okaloosae — Carr and Goin, 1955:100 (characters and range mixed with that of *E. swaini*); Neill, 1957:185 (endemic in Florida panhandle); Yerger, 1960: 41 (validity of species, range).

Etheostoma swaini—in part; Bailey, Winn, and Smith, 1954: 143-144 *(E. okaloosae* synonymized with *E. swaini);* Moore, 1957:195 *(E. okaloosae* included under *E. swaini).*

Type—Holotype ANSP 69159; 24.4 mm female; Fla., Okaloosa Co., Little Rocky Cr., 7 mi. NE of Niceville on rt. 218 (now Fla. 285); June 20, 1939; F. Harper.

Since Fowler (1941:242) omitted counts of the cephalic pores, the following should be added to the original description (from examination of the holotype by the senior author): supratemporal canal complete, infraorbital with 8 pores, preoperculomandibular with 9 pores, both interorbital pores and coronal pore present. Counts of the lateral-line scales differ from Fowler's account of 30+3=33; there are 33+3=36 on the left and 35+2=37 on the right.

Comparisons—Etheostoma okaloosae is compared with *E. edwini* in Table 1. As previously indicated, it appears to be somewhat intermediate between *E. edwini* and *E. (Oligocephalus) swaini,* with which it has been confounded. *E. okaloosae* differs from *E. swaini* in the much shorter and more rugose genital papilla of the female (Fig. 7); in the higher arch in the lateral line, in the slenderer caudal peduncle, in the smaller number of unpored lateral-line scales, and in various details of pigmentation (Figs. 1-6); in having the preopercular margin at least slightly crenulate; and the prepectoral area at least partly scaled. *E. okaloosae* usually has 9 preoperculomandibular pores while both *E. edwini* and *E. swaini* usually have 10.

Coloration—On the first dorsal fin of the non-breeding female small to medium-sized melanophores are arranged in two or three irregular bands. The membrane of the soft dorsal fin is clear, with dark spots in four to six (usually four) rows. On the anal fin a few small melanophores are scat-

TABLE 1.
Comparison of Etheostoma edwini and E. okaloosae

Character	*E. edwini*	*E. okaloosae*
Branchiostegal membranes	Separate	Narrowly conjoined
Unpored lateral-line scales	4-18 (usually 7-15)	0-4
Pored lateral-line scales	20-34 (usually 23-32)	30-36 (usually 32-34)
Total lateral-line scales	34-42 (usually 36-40)	32-37 (usually 34-35)
Preoperculomandibular pores	Usually 10 (but often 9, and usually 9 in the Ochlockonee drainage)	Usually 9
Preopercular margin	Entire	At least slightly crenulate
First anal spine	Shorter than second	Longer than second
Red spots on body of males in life	Conspicuous	Lacking

tered, chiefly on the basal portion, occasionally on the rays. The rays of the pectoral fins are indistinctly outlined with pigment cells, which may also be scattered on the rays. The pelvic fins are similar to the pectoral fins. The caudal fin is indistinctly barred with five dark bands. The interradial membranes are clear or have a few melanophores on their distal portions. The belly and breast are usually immaculate white, but may possess a few brownish chromatophores. The cheek, throat, chin and branchiostegal membranes are usually white with numerous freckles formed by clusters of medium to large melanophores. All four orbital bars are developed. The supraorbital enters the eye. The suborbital is slightly to moderately developed and rarely enters the eye. The snout is almost uniformly pigmented. A single, median black spot is present at the base of the caudal fin and diffuse, brownish spots usually occur dorsal and ventral to the median spot. A well defined black spot covers one to two and one-half scales in the humeral region. Lateral-line scales are pigmented like the scales above and below, but the pores are unpigmented and appear as a thin, light-colored line. Excluding the humeral and basi-caudal spots, a series of 9-11 (usually 9) rectangular lateral blotches, wider than high, are located immediately below the lateral line. Dorsal spots or saddles are absent or indistinct; if present, two are on the nape, three under the first dorsal, two to four under the soft dorsal, and one, rarely, at

TABLE 2.
Number of pored lateral-line scales in Etheostoma edwini and E. okaloosae [1]

Species and Drainage	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	N	x̄
E. edwini																			
St. Johns							3	10	7	4	5	1						30	28.03
Suwannee							4	5	10	15	13	10	11	4	3			75	29.87
Ochlockonee			1	—	—	2	7	18	20	8	8	6	5	1				76	28.30
Apalachicola																			
Flint				1	4	9	12	27	14	7	—	2	2					78	27.00
Chattahoochee				1	3	5	6	3	2	3								23	26.09
Chipola	1	4	6	13	26	14	18	3	5	—	2	—	1					93	24.62
Total Apalachicola	1	4	6	15	33	28	36	33	21	10	2	2	3					194	25.75
West of Apalachicola																			
Choctawhatchee	1	1	2	8	13	27	40	25	12	3	1	—	1					134	25.79
Pensacola Bay					2	5	10	17	21	7	11	3	—	—	1			77	27.79
E. okaloosae							1	4	6	1								12	27.58
Perdido											3	4	19	27	19	6	2	80	33.01

[1] To eliminate developmental variation, counts on specimens below 22 mm. have not been used.

TABLE 3.
Number of unpored lateral-line scales in Etheostoma edwini and E. okaloosae

Species and Drainage	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	N	x̄
E. edwini																					
St. Johns								1	4	4	6	12	2	1	—	—	1			31	10.32
Suwannee					1	3	6	11	15	19	13	4	1	1						74	9.41
Ochlockonee					4	6	3	8	12	23	10	5	3	1	1					76	8.43
Apalachicola																					
Flint						2	—	1	10	16	19	13	7	4	3	2				77	10.16
Chattahoochee								1	1	7	3	8	1	2	5	2				30	11.13
Chipola								2	1	1	2	12	14	20	29	9	7	2		99	13.11
Total Apalachicola						2	—	4	12	24	24	33	22	26	37	13	7	2		206	11.72
West of Apalachicola																					
Choctawhatchee							1	—	2	7	19	42	29	20	15	4	1	3	1	144	11.81
Pensacola Bay					1	1	4	5	9	21	13	12	9	1	2					78	9.49
Perdido									3	4	4	1								12	10.25
E. okaloosae	5	33	26	12	4															80	1.71

the origin of the first caudal ray. The sides of the body are marked with longitudinal rows of dark dots, which extend from head to tail. There are two or three rows above and three to five rows below the lateral line. The center of each scale bears a pigment spot which is darker than the remainder of the scale. The genital papilla is usually immaculate, but occasionally a patch of melanophores appears posterior to its base. In breeding females there is a general increase in the number of small melanophores over most of the body and fins, and the submarginal orange-red band in the first dorsal becomes brighter. Figure 2 illustrates a female in breeding condition.

In the non-breeding male the pigmentation of the pectoral fins, orbital bars, snout, basi-caudal spots, humeral spot, lateral blotches, and longitudinal rows of dots is very similar to that of the female. Melanophores are more numerous on the first dorsal, anal, pelvic, and caudal fins. One-half to seven-eighths of the anal and pelvic fin membranes are darkened by these melanophores. The second dorsal fin is dark with light spots, just opposite to the condition in the female. The belly, breast, cheek, throat, and branchiostegal membranes possess numerous small melanophores. The genital papilla is immaculate, except for a few small melanophores around the base posteriorly.

The pigmentation of the breeding male is characterized by an enormous increase in the number of small melanophores over the entire body and fins. The submarginal orange-red band on the first dorsal fin is more vivid. Numerous melanophores are concentrated between spines VIII and IX to form two dark blotches. The anal fin is darkened by numerous melanophores, and one or two blotches are frequently evident between the first and second or between the second and third soft-rays. Melanophores are present on the basal one-third to one-half of the pectoral fin membranes. The pelvic fins are dusky, with an occasional blotch. The barring on the caudal fin may be indistinct, and the entire membrane is speckled with tiny melanophores. The presence of more melanophores on the lateral line renders the pores less distinct than in non-breeding individuals. The lateral blotches usually become more promi-

TABLE 4.
Total number of lateral-line scales in Etheostoma edwini and E. okaloosae

Species and Drainage	32	33	34	35	36	37	38	39	40	41	42	N	x̄
E. edwini													
St. Johns						7	18	6	1	1		33	38.12
Suwannee					2	1	13	27	22	8	3	76	39.34
Ochlockonee				5	25	44	5	4	1			84	36.77
Apalachicola													
Flint			3	5	13	30	24	8	1			84	37.13
Chattahoochee					4	12	4	3	2			25	37.48
Chipola					9	40	46	15		2		112	37.67
Total Apalachicola			3	5	26	82	74	26	3	2		221	37.44
West of Apalachicola													
Choctawhatchee				1	15	53	46	14	5	2		136	37.59
Pensacola Bay			1	1	11	25	29	10	3			80	37.53
Perdido						5	4	4		1		14	38.14
E. okaloosae	1	6	24	34	13	1						79	34.70

TABLE 5.
Number of scale rows above and below the lateral line in Etheostoma edwini and E. okaloosae

	Above the lateral line						Below the lateral line								
Species and Drainage	2	3	4	5	N	x̄	5	6	7	8	9	10	11	N	x̄
E. edwini															
St. Johns		16	5		21	3.24		2	15	4				21	7.10
Suwannee		22	40	1	63	3.67		4	11	24	20	4		63	8.14
Ochlockonee		15	56	5	76	3.87		10	40	23	3	1		77	7.29
Apalachicola															
Flint		38	39	2	79	3.54		21	42	15	1			79	6.95
Chattahoochee	2	13	10		25	3.32	1	6	15	3				25	6.80
Chipola		44	20		64	3.31	1	8	19	20	11	3	1	63	7.71
Total Apalachicola	2	95	69	2	168	3.42	2	35	76	38	12	3	1	167	7.22
West of Apalachicola															
Choctawhatchee	2	86	50		138	3.35	1	43	75	19				138	6.81
Pensacola Bay	1	58	23		82	3.27	4	42	29	6	1			82	6.49
Perdido		12	2		14	3.14		10	3	1				14	6.36
E. okaloosae		10	70		80	3.88	5	74						79	5.94

nent, increase in size, become deeper than wide, and extend above the lateral line to within one or two scale rows of the dorsal fin, as well as below the lateral line. In some specimens these lateral blotches are barely discernible. The darkened appearance of the fish in breeding color renders the longitudinal rows of dots on the sides of the body less distinct. Melanophores are formed on the margins of the upper and lower surfaces of the genital papilla, as well as on the basal portion. Other areas are similar but darker than in the non-breeding male. Figure 5 shows the pattern of a male in breeding condition.

In life, the colors are far less striking than in *E. edwini.* The general color of the adult male is reddish-brown to yellow-brown, becoming lighter on the lower flanks and yellow-white to dusky white on the throat. An olive-green cast is especially prominent below the lateral line and on the caudal peduncle. The areas around the bases of the pectoral and pelvic fins are golden-yellow. The margin of the first dorsal is dusky with a bright submarginal orange-red stripe. The basal two-thirds of the fin is dusky. The membranes of the dorsal and pelvic fins are dusky with a papilla of a typical female of *E. okaloosae* is fin is usually barred with vertical bands of light and reddish brown, the dark bands are the broader. Females generally resemble the males, but the fins and body are lighter, and the orange-red stripe in the spinous dorsal is less bright.

Genital Papilla—In breeding females, the genital papilla is very similar to that of *E. edwini,* except that the tube is somewhat longer. Misuse of an air jet or excessive probing will create the appearance of free villi, as in *E. edwini.* The genital papilla of a typical female *E. okaloosae* is compared with that of *E. edwini* and *E. swaini* in Figure 7.

Development—Development in *E. okaloosae* is probably similar to that in *E. edwini.* Two 15 mm specimens have only 22 and 28 pored lateral-line scales while all specimens over 20 mm long have at least 32. Both 15 mm specimens have incomplete supratemporal canals, ten specimens 17.5-20.0 mm long are equally divided between incomplete and complete, and almost all specimens over 20 mm long have complete canals.

Habitat—The terrain in that portion of Okaloosa and Walton counties inhabited by *E. okaloosae* is sandy, deeply dissected, and covered by pines, scrub oaks and mixed hardwoods. Stream valleys are marked by the presence of alder, titi, wax myrtle, blackgum, and pines and oaks. The clear streams are small to medium-sized, with a moderate to swift current. The bottom consists chiefly of clean, light-colored sand, with some mud and detritus around patches of vegetation in areas with reduced circulation. Depths vary from six inches to four feet, and widths from five to 40 feet. The water is nearly neutral or slightly acid (pH 6.6-6.9). Vegetation is absent in some areas, sparse and scattered where clumps of bullrushes *(Scirpus etuberculatus)* are found, or dense with *Mayaca, Orontium, Nuphar, Nitella,* and *Potamogeton capillaceus.* The red alga, *Batrachospermum,* is present throughout the year, and occasionally forms thick concentrations. Other common fishes in these streams included: *Ichthyomyzon gagei, Esox americanus, Erimyzon sucetta, Notropis hypselopterus, N. petersoni, Hybopsis harperi, Noturus leptacanthus, Gambusia affinis, Aphredoderus sayanus, Micropterus salmoides, Ambloplites rupestris ariommus, Lepomis punctatus,* and *Percina nigrofasciata.*

Habits—The two species of darters in this stream system occupy different niches. *Etheostoma okaloosae* is most common around clumps of the bullrush *(Scirpus)* over a clean sandy bottom in areas with reduced current. It is usually in water from six inches to two feet deep and has rarely been collected at depths of three feet or greater. Few specimens have been taken from sections of the stream where *Mayaca* and other aquatic plants provide dense cover. Apparently this species avoids the large amounts of silt and organic sediments that accumulate in these heavily vegetated areas.

The other darter, *Percina nigrofasciata,* frequents the swifter areas of the stream, in the channels and deeper pools where vegetation is sparse or absent, but where logs or brushy cover are available. Only occasionally is it taken in areas with little water movement.

E. okaloosae was observed spawning by W. Bruce Walden and Ray Birdsong in Tom's Creek on March 25, 1961, in the swiftest part of the stream in water 12 to

TABLE 6.
Number of first dorsal spines and second dorsal rays in Etheostoma edwini and E. okaloosae

	First dorsal spines						Second dorsal rays					
Species and Drainage	8	9	10	11	N	$\bar{x}$	9	10	11	12	13	N	$\bar{x}$
E. edwini													
St. Johns		9	16	1	26	9.69		1	19	6		26	11.19
Suwannee	1	27	33	1	62	9.55		6	34	20	2	62	11.29
Ochlockonee	2	47	34	1	84	9.40		18	59	7		84	10.87
Apalachicola													
Flint	9	53	17		79	9.10	1	14	39	23	2	79	11.14
Chattahoochee	6	17	2		25	8.84	1	4	8	11	1	25	11.28
Chipola	5	44	15		64	9.16	4	35	22	3		64	10.38
Total Apalachicola	20	114	34		168	9.08	6	53	69	37	3	168	10.87
West of Apalachicola													
Choctawhatchee	15	98	22	1	136	9.07	1	72	58	6		137	10.50
Pensacola Bay	14	60	9		83	8.94		22	49	10	2	83	10.90
Perdido		13	1		14	9.07		3	8	3		14	11.00
E. okaloosae	2	31	4		37	9.05		3	32	40	5	80	11.59

TABLE 7.
Number of pores in the infraorbital and preoperculomandibular canals in Etheostoma edwini and E. okaloosae

	Infraorbital pores							Preoperculomandibular pores					
Species and Drainage	6	7	8	9	10	N	$\bar{x}$	8	9	10	11	N	$\bar{x}$
E. edwini													
St. Johns			12	3		15	8.20	1	7	11	1	20	9.60
Suwannee		2	38	2	1	43	8.05	1	26	33	1	61	9.56
Ochlockonee		4	75	4		83	8.00	3	70	5		78	9.03
Apalachicola													
Flint		8	75	1		84	7.92	2	14	62	1	79	9.78
Chattahoochee		1	21	2		24	8.04			24		24	10.00
Chipola		5	55	5	1	66	8.03		2	57		59	9.97
Total Apalachicola		14	151	8	1	174	7.98	2	16	143	1	162	9.88
West of Apalachicola													
Choctawhatchee	1	6	124	6	1	138	8.00	1	24	108	4	137	9.84
Pensacola Bay		12	69	1		82	7.87	3	18	54		75	9.68
Perdido		1	13			14	7.93		2	12		14	9.86
E. okaloosae		2	39			41	7.95	1	46	4		51	9.06

TABLE 8.
Number of anal soft rays and squamation of nape in Etheostoma edwini and E. okaloosae

	Anal soft-rays							Nape squamation*				
Species and Drainage	5	6	7	8	9	N	$\bar{x}$	I-C	I/PX-C/T	PX-T	PX/X-T	X-T
E. edwini												
St. Johns		4	14	3		21	6.95					
Suwannee		13	29	3		45	6.78	1	6	2	1	
Ochlockonee	1	31	43	3		78	6.62		7	1	3	
Apalachicola								1	5	7	2	
Flint		8	41	29	1	79	7.29	1	15	3		
Chattahoochee	1	4	13	6	1	25	7.08		7	6	1	
Chipola	1	34	25	3	1	64	6.52		1	3	5	2
Total Apalachicola	2	46	79	38	3	168	6.96	1	23	12	6	2
West of Apalachicola												
Choctawhatchee	2	70	62	4		138	6.49		1	—	1	7
Pensacola Bay		31	49	3		83	6.66		1	1	—	9
Perdido			10	4		14	7.29					3
E. okaloosae		8	65	7		80	6.99	5	26	1		

*See Text, page 223.

18 inches deep over a sandy bottom at the edge of clumps of *Nitella*. The male mounted the back of the female. Then, while remaining in a horizontal position, both moved forward a short distance, paused, and moved again. The pair spawned a few moments later, while lying side by side. Both male and female rotated their bodies slightly until their ventral surfaces were opposed, and quivered for several seconds. Examination of the vegetation revealed that several eggs had been deposited singly within the branches of *Nitella*. The vegetation and eggs were taken to the laboratory where one 5.5 mm larva hatched on March 27.

Several mature adults captured on March 25 were placed in aquaria in the laboratory. Although spawning behavior was not witnessed, six eggs were discovered on April 1, individually attached to masses of *Nitella*.

This spawning behavior is quite different from that observed by Winn (1958: 173) for other darters, where species with

flattened, flower-like genital papillae demonstrated a complex, inverted spawning behavior and laid their eggs on the underside of rocks.

Examination of adult females collected in January, March, August, September, and October revealed that large ova were present from late January to early August. The smallest young (15 mm SL.) in existing collections were taken August 11 and September 9. Breeding coloration appears to be most highly developed in January and March collections. It seems likely that this species has a rather long breeding period, probably from midwinter through early summer. The onset of spawning may vary from year to year, for temperature conditions in January and February in western Florida are mild in some years and severe in others.

Males are larger than females but the difference appears to be less than in *E. edwini*. The largest male of *okaloosae* examined is 43.5 mm long and the largest female 40.0 mm (both FSU 6078, Tom's Cr.). Differences in sexual coloration are likewise less pronounced. Although these differences in size and coloration are slight, limited observations both in the field and in aquaria indicate that this species exhibits territorial behavior to some extent. Studies on the reproductive behavior of both species of *Villora* are being continued by the junior author.

Distribution—*E. okaloosae* is confined to those streams of Okaloosa and Walton counties in west Florida that empty into Rocky and Boggy bayous near the western end of Choctawhatchee Bay, in the vicinity of Niceville. From east to west these streams are known as Rocky Creek, Lone Creek, Swift Creek, Turkey Creek, Tom's Creek, and their various tributaries. Although several of the streams inhabited by *E. okaloosae* originate less than a mile from the headwaters of streams inhabited by *E. edwini*,

Figure 10. Distribution of *Ethcostoma edwini* (dots) and of *E. okaloosae* (open circles; encircled dot is the type locality) in the Choctawhatchee Bay region of western Florida. The stippling indicates the area of the hypothetical Pleistocene peninsula or island (see text) above the 150-foot contour line.

the two species are allopatric. The greatly restricted range of *E. okaloosae* is encircled by the range of the much more widely distributed *edwini* (Figs. 9 and 10). The collection sites for the specimens examined in this study together with the distribution of adjacent populations of *E. edwini* are shown in Fig. 10.

A slight lowering of sea level during Pleistocene glacial stages would have resulted in the conjoining of all the creeks inhabited by *E. okaloosae* into a single stream system originating in a highland area a few miles north of the Gulf of Mexico. The stippling on Fig. 10 indicates the land areas above the 150-foot contour line, which according to MacNeill (1957), is the maximum height to which sea-level rose during Pleistocene interglacial stages. It is likely, then, that during maximum inundation of the Coastal Plain, a peninsula with a very narrow connection to the mainland, or possibly an island, with freshwater drainage would have remained above the sea, and served as a refuge for *E. okaloosae* and other freshwater and terrestrial species. Cooke (1945) postulated a maximum rise of the sea to the present 270-foot contour. Even if this were the case, some land would have been emergent, for elevations up to 294 feet occur along this high ridge. Under these conditions, an island would have been cut off from the mainland to the north. Since erosion has continuously lowered this land mass, elevations in the Pleistocene were undoubtedly considerably higher, and consequently the highlands would have been greater in area than at present.

During one of the oscillations of sea-level in the Pleistocene, the *Villora* population in the stream system now inhabited by *okaloosae* may have been cut off from other *Villora* populations in the Choctawhatchee River drainage. During this period of isolation, a series of mutations may have occurred and may have spread rapidly through this small inbred population. Since the headwaters of this stream system would have remained above the sea, differentiation might have been completed prior to the subsequent lowering of sea-level to the point where the differentiated population may again have come in contact with older *Villora* populations. In the meantime, the ancestral *Villora* stock would have been forced into the headwaters of adjacent streams, and with the lowering of sea-level, could have moved downstream into newly emerged habitats to the west, north, and east (in the Yellow, Shoal, and Choctawhatchee rivers), and thereby have surrounded the range of *E. okaloosae.*

TABLE 9.

Proportional measurements of adults of Etheostoma edwini and E. okaloosae in thousandths of standard length

Catalog Number, FSU	*E. edwini* 4799 (5 females) 6178 (3 males) 4950 (2 males)		*E. okaloosae* 5135 (3 males, 1 female) 5138 (2 males, 1 female) 6214 (3 females)	
Measurement	Range	$\bar{x}$	Range	$\bar{x}$
Standard length, mm	29.7 - 43.6	36.3	28.7 - 39.9	33.4
Head length	256 - 302	280 6	268 - 323	292.6
Greatest depth	197 - 228	212.7	200 - 235	215.2
Least depth	95 - 115	105.8	109 - 153	123.5
Body width	128 - 157	143.4	131 - 164	146.3
Caudal peduncle length	280 - 350	299.7	245 - 272	260.2
Highest dorsal spine	109 - 158	131.3	106 - 135	123.2
Highest dorsal soft-ray	140 - 174	153.0	137 - 153	145.7
Caudal length	221 - 249	231.3	205 - 221	213.4
First anal spine	71 - 93	79.6	85 - 120	94.5
Second anal spine	76 - 95	86.7	70 - 105	84.4
Highest anal soft-ray	135 - 194	151.0	132 - 155	142.8
Longest pectoral ray	241 - 269	255.4	246 - 273	255.1
Pelvic length	196 - 212	206.4	194 - 223	205.7
Pelvic base	26 - 35	29.6	30 - 37	32.8
Interpelvic distance	11 - 17	14.5	12 - 18	14.6
Head depth	165 - 185	162.8	163 - 186	172.1
Head width	139 - 167	155.0	151 - 173	162.2
Snout length	41 - 60	50.2	48 - 64	57.6
Orbit length	71 - 90	79.5	72 - 81	75.9
Fleshy interorbital width	51 - 60	55.0	46 - 62	55.4
Upper jaw length	70 - 79	74.7	64 - 88	80.2
Distance from tip of jaw to union of gill membranes	104 - 139	117.9	137 - 161	150.0
Distance from union of gill membranes to insertion of pelvic fin	146 - 191	165.1	135 - 165	150.5

However, a comparison of primitive and specialized characters in the two species of *Villora* indicates that *E. okaloosae* is the more primitive species. It has a more nearly complete lateral line and a deeper body, the genital papilla of the breeding female is not quite as specialized, and the male lacks red spots on the body. If it evolved at an earlier date than *E. edwini*, it is reasonable to assume that it formerly occupied a wider range, which was later restricted by changes in sea-level during the Pleistocene, and that today it persists only as a relict. Its presence in only one stream system tributary to Choctawhatchee Bay is definitely believed to be related to the Pleistocene peninsula or island conditions described previously.

The unusual distributional patterns of many plant and animal species in the Florida panhandle have been discussed by Neill (1957). The occurrence of a number of endemics and "northern disjuncts" in Okaloosa and Walton counties on or in proximity to the Pleistocene peninsula or island emphasizes the unusual ecological conditions prevailing there. Recent unpublished investigations have added several species to this list. Further investigations on these problems are in progress by the junior author.

Specimens Examined—Since *E. okaloosae* was heretofore known only from the type locality, complete data are given. All series are from the Choctawhatchee Bay drainage system of western Florida.

Rocky Creek—Walton Co.: FSU 6101 (6 specimens, 24-32 mm. in standard length), E. Rocky Cr., 11.2 (airline) mi. NE Niceville, on Eglin Air Force Base rd. 201, Jan. 24, 1960. FSU 6032 (2, 27-30), Rocky Cr., 7.75 (airline) mi. NE Niceville on EAFB 200, Jan. 24, 1960. Okaloosa Co.: Little Rocky Cr., 7.5 mi. NE of Niceville on Fla. 285, type locality; ANSP 69159 (1, 24), holotype, June 20, 1939; FSU 6045 (25, 23-39), Jan. 23, 1960. UF 6937 (2, 23), Big Rocky Cr. near Niceville, Nov. 13, 1938.

Lone Cr.—Okaloosa Co.: FSU uncat. coll., Lone Cr., 4 mi. E Niceville, Feb. 4, 1961.

Swift Creek—Okaloosa Co.: FSU 5158 (7, 26-40), Swift Cr., 1.2 mi. NE Niceville on Fla. 285, Sept. 9, 1959.

Turkey Creek-Okaloosa Co.: FSU 5135 (26, 15-35), Turkey Cr., 5.4 mi. NW Niceville on EAFB 232, Sept. 9, 1959. Tenmile Cr., 3.5 mi. NW Niceville on Fla. 85: USNM 196136 (10, 23-39), Oct. 19, 1960; TU 18364 (3, 27-34), May 31, 1958. Turkey Creek, at W edge of Niceville on Fla. 85: FSU 1937 (1, 28), May 24, 1953; FSU 6214 (21, 15-33), Aug. 11, 1959; TU 4716 (1, 25), Nov. 14, 1952.

Tom's Creek - Okaloosa Co.: Tom's Creek approx. 2 (airline) mi. W Valparaiso on Fla. 85; FSU 6078 (50, 30-44), Jan. 25, 1960; FSU 6138 (11, 31-43), Mar. 26, 1960; FSU 6748 (10, 25-40), Oct. 19, 1960; TU 2079 (3, 28-38), May 26, 1951.

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VI. Abstract

The subgenus *Villora* Hubbs and Cannon is removed from *Hololepis* Putnam where it has been placed by some authors. This decision is based upon the belief that *Villora* constitutes a separate phyletic line running somewhat parallel to *Hololepis* and probably originating from the subgenus *Oligocephalus*. Important differentiating characters of *Villora* include lack of breeding tubercles, moderately arched lateral line, genital papilla of breeding female a low tube crowned with villi, a prominent humeral spot and a somewhat incomplete lateral line.

Variation in a number of meristic characters between populations of *Etheostoma (Villora) edwini* (Hubbs and Cannon) is considered. Three slightly differentiated races of *edwini* may be distinguished using lateral-line scales, preoperculomandibular pores and squamation of the nape. This species occurs in nothern and western Florida and below the Fall Line in southwestern Georgia and in Alabama.

E. okaloosae (Fowler) is resurrected from the synonomy of *E. swaini* (Jordan). It differs from *E. (Oligocephalus) swaini* in number of preoperculomandibular pores, shape of the genital papilla of breeding females, arching of the lateral line, squamation of the breast, nape, and prepectoral area, and in habitat. Several of these characters show that *E. okaloosae* is most closely related to *E. edwini* and belongs to the subgenus *Villora*. Possible reasons for the isolation of *E. okaloosae* in several small streams tributary to one arm of Choctawhatchee Bay are discussed and it is concluded that this is a relict species.

Photographs of both species and figures of the genital papillae are presented along with those for *E. swaini*. Discussions of habits, habitat, and relationships are included.

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Ability of Salmonids to Ascend High Fishways[1]

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ABSTRACT

The ability and persistence of salmonids in ascending pool-and-overfall fishways was measured in experimental "endless" fishway structures in which fishways of any height could be simulated. Six chinook salmon (*Oncorhynchus tshawytscha*), four sockeye salmon (*O. nerka*), and four steelhead trout (*Salmo gairdneri*) were permitted to ascend 1,000 feet in the experimental fishways. One sockeye salmon was allowed to ascend an endless fishway for over 5 days, climbing 6,648 feet, a vertical ascent of more than a mile, before the test was discontinued. Rate of ascent of all fish tested increased following an initial period of experience in the fishway. The level of blood lactate in the exercised fish showed no evidence of fatigue. Practical significance of the data in relation to fishway design is discussed.

INTRODUCTION

The large-scale development of water resources on the Columbia River system, with construction of numerous large dams on the main river and tributary streams, poses many special problems for agencies responsible for providing safe passage for migrant anadromous fish. One of these problems is the design of fishways for adult migrants at high dams. Experience on the Columbia River has been confined to fishways requiring a total vertical ascent of less than 100 feet. McNary Dam, the highest dam with fishways on the Columbia, requires an ascent of 92 feet. Pelton Dam on the Deschutes River, a tributary of the Columbia, has fishways requiring a total ascent of 338 feet, although this height is attained gradually over a distance of almost 3 miles. Several dams now proposed, however, would require that fish ascend much greater heights. The question arises as to whether the pool-and-overfall fishways now conventional on the Columbia River would be practical with dams 300, 400, or 500 feet high, or whether the migrating fish would tire after a few hours and fail to complete passage through such fishways.

Another concern is the possibility that migrating fish might become fatigued because the effects of ascending fishways at many dams accumulated. In the Columbia River adult migrants may have to ascend as many as 10 major dams before reaching their spawning areas. Whether or not a total ascent of as much as 1,000 feet in pool-and-overfall fishways would fatigue fish to the degree that they might be unable to reach spawning areas or to reproduce successfully has been a matter of apprehensive speculation.

In an attempt to provide at least partial answers to these and other questions related to the behavior and performance of migrating fish in pool-and-overfall fishways, a series of tests was made in specially designed experimental structures in which fishways of great height could be simulated.

MATERIALS AND METHODS

The experiments were conducted in the Fisheries-Engineering Research Laboratory at Bonneville Dam on the Columbia River using a pair of "endless" fishways. These experimental fishways were pool-and-overfall types constructed so that each made a complete circuit (Figure 1), with the highest pool con-

[1] Research financed by the U. S. Army Corps of Engineers as a part of a broad program of Fisheries-Engineering Research for the purpose of providing design criteria for fish-passage facilities at Corps projects on the Columbia River.

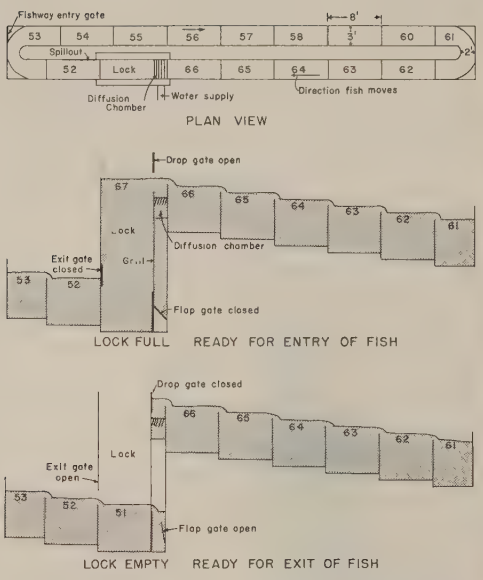

FIGURE 1.—Diagram of the 1-on-8-slope endless fishway showing plan and side views of two phases of lock operation. Numbers 51 through 67 are pool elevations in feet above mean sea level.

nected to the lowest pool by means of a lock. When a test fish had ascended to the top of one of these fishways it was rapidly locked to the lowest pool to begin its ascent again. By repeating the procedure, fishways of any desired height could be simulated. Two endless fishways were constructed in order to study the effect of fishway slope on the performance and biochemistry of the ascending fish. Results of that study, with related observations on the effects of pool hydraulics on patterns of ascent, will be reported elsewhere.[2] This report is confined to the aspect of extended ascents of 1,000 or more feet.

One of the endless fishways had a slope of 1 on 8 (Figure 2) with pools 8 feet long, 3 feet wide, 6.8 feet deep and with overfalls of 1 foot between pools. The other fishway, with a 1-on-16 slope (Figure 3), was similar except that the pools were 16 feet in length. The locks in both fishways were 8 feet long, 3 feet wide, and 23 feet deep when filled and 7 feet deep when drained (Figure 1). Weirs in both fishways were 6 feet high, 2 inches thick, with flat crests and were without orifices through

[2] Collins, Gerald B., Carl H. Elling, Joseph R. Gauley, and Clark S. Thompson. Effect of fishway slope on the performance and biochemistry of salmonids. (Manuscript in preparation.)

FIGURE 2.—The 1-on-8-slope endless fishway shown during construction. Locking unit for lowering and recycling fish appears in center. Entry gate (shown closed) is visible in foreground.

which fish might pass. Water flow over the weirs was maintained by 0.8 foot of head measured 2.5 feet upstream from the weir crest. Turn pools were larger in volume than the other pools in the fishway (Figure 1) since pool length in the turn pools was measured on the straight sections of the inside wall. During the initial test in 1958, a wooden grill was placed in each turn pool to restrict fish movements to the upper 2 feet in order to reduce the tendency of fish to linger in these pools. In the second year the grills were covered with plywood, and turbulence-creating baffles were installed to make the turn pools unsuitable as resting areas. In order to modify the hydraulic conditions in the pools of the 1-on-8-slope fishway, weir crests were reduced in width from 36 inches to 26 inches during the second year, reducing pool turbulence and introducing lateral eddies in the pools. The differences in pool hydraulic pattern, in fishway slopes, in weir crests, and in turn pools

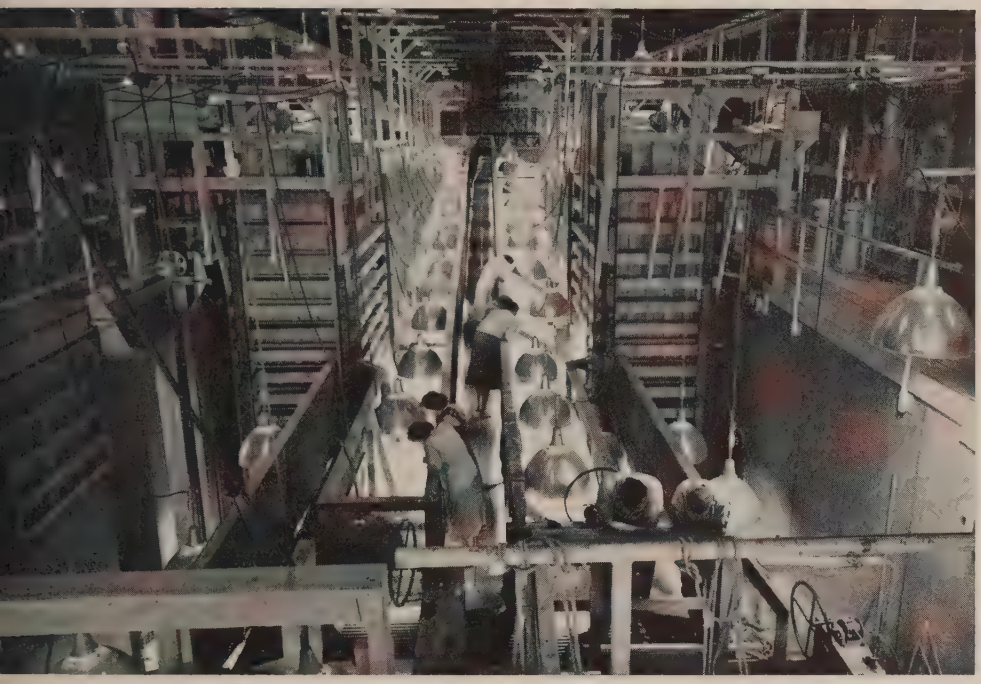

FIGURE 3.—The two endless fishways in operation. Observers on walkways record progress of fish.

re called to attention to emphasize the variety f conditions under which the extended as- ents were made. Throughout each individual est, however, constant conditions were main- ained.

Light was supplied by 1,000-watt mercury- apor lamps suspended 6 feet above the water urface and 6 feet apart along the fishway. These lights were on day and night, producing n average light intensity of 800 foot candles t the water surface.

PROCEDURE

As in all of the experiments conducted at he Fisheries-Engineering Research Labora- ory (Collins and Elling, 1960), the experi- nental fish were not handled in any way prior o testing. Fish were permitted to swim into he laboratory from the adjoining fishway and nto a small collection pool. Then, when an ntrance gate (Figure 2) was opened, fish wam from the collection pool into one of the ndless fishways to begin the ascent. Once a ish had entered an experimental fishway, the ntrance gate was closed and the fishway was perated as a closed system until the comple- ion of the test. Observers followed the prog- ress of each test fish at all times(Figure 3), recording the time each weir was crossed, and in this way obtained a detailed record of the time spent in each pool throughout the entire test. Because of the necessity for synchroniz- ing locking with the movements of the fish, all tests were made with individual fish. Upon completion of a test, water flow was shut off, the fish was netted, and blood and tissue sam- ples were taken for biochemical studies. Sex, weight, and length were then determined.

RESULTS

The first attempt to measure the maximum height that a salmon would ascend in a pool- and-overfall fishway was made in 1958 with a sockeye salmon (*Oncorhynchus nerka*). That fish, a 20-inch male weighing 3 pounds 4 ounces, was allowed to ascend the 1-on-8-slope endless fishway for over 5 days. It ascended day and night, climbing 6,648 feet in 7,947 minutes, an average of 1.2 minutes per pool. It completed 415 circuits in the endless fish- way, traveling slightly more than 10 miles horizontally while ascending more than a mile vertically, and it was still actively ascending the fishway when the test had to be discon-

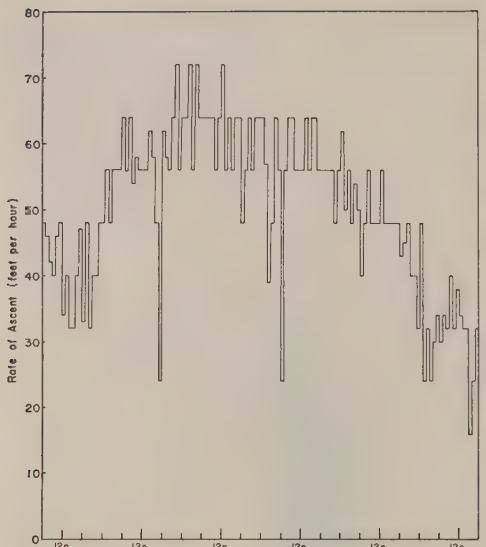

FIGURE 4.—Performance of a sockeye salmon (*O. nerka*) ascending the 1-on-8-slope endless fishway during July 1–6, 1958. The fish was still actively ascending when the test was terminated.

tinued because of other experimental commitments.

An examination of the rate of ascent during the test (Figure 4) reveals that performance actually increased the first 2 days and that it was not until the fifth day, after the fish had ascended more than 6,000 feet, that the rate of ascent dropped below that of the first day. The increased rate of ascent in the first couple of days could probably be attributed to learning. McLeod and Nemenyi (1940) state that in their experimental fishways trout apparently learned to climb fish ladders. The gradual decline in the rate of ascent in the last 2 days of the test might be ascribed either to a gradual loss of interest in the often-repeated cycle of events or to changes in the physical condition of the fish.

Blood-lactate level, frequently used as an index of muscular fatigue (Black, 1958), however, was only 32.88 milligrams percent in the sockeye salmon after its long ascent of more than 6,000 feet. This level is well below the 125 milligrams percent that Parker and Black (1959) found to be minimum for lethal effects in troll-caught salmon. It is also less than the mean lactate level (63.5 milligrams percent)[3]

[3] Details of data, sampling techniques, and chemical methods are reported elsewhere. See footnote 2.

FIGURE 5.—Sockeye salmon after an ascent of 6,648 feet in the 1-on-8-slope endless fishway. Note fungus on head and abrasions on the side.

of all the sockeye salmon that were tested with an ascent of 104 feet in the 1-on-8-slope fishway during 1958.

Water temperature in the endless fishway increased from 64° F. at the start of the test to 67° F. on the final day. Whether or not this rise in temperature affected the rate of ascent in any way is not known.

During the prolonged ascent several changes in the external appearance of the fish were noted. No marks, abrasions, or fungus were apparent when the fish was first admitted to the fishway nor were they apparent during the first 2 days of the ascent. However, on the third day two small white spots were seen on the top of the head and another on the left side of the fish near the adipose fin. On the fourth day these had grown in size and a fungus growth was beginning to show near the insertion of the dorsal fin. Lesions had appeared on the right side of the fish by the fifth day and by the final day the top of the head was covered with fungus, the tail had become frayed and the lesions on the side of the fish had grown in size (Figure 5). Such injuries give evidence of physical contact with the fishway structure, possibly the result of the tendency of individual fish to cross weirs next to a wall (Collins, 1958). Irritation from these injuries could have been a contributing factor in the decline in the rate of ascent noted in the final days of the test.

To determine whether the ability and persistence shown by the first salmon given an opportunity for a prolonged ascent in an endless fishway were characteristic of salmonids in the Columbia River, a series of extended ascent tests was made during the migration of 1959. These tests were arbitrarily limited to 1,000 feet in order to conserve time and allow testing of a larger number of fish. The ex-

ABLE 1.—*Ascent time and lactate level of whole blood (milligrams percent) for chinook salmon* (O. tshawytscha), *sockeye salmon* (O. nerka), *and steelhead trout* (S. gairdneri) *ascending 1,000 feet in experimental endless fishways, 1959*

Date	Species	Sex	Weight (pounds)	Gonad weight as percentage of body weight	Fishway slope	Water temperature (° F.)	Ascent time (minutes)	Lactate whole blood (milligrams percent)
ne 15, 16	Chinook	F	22	5.63	1 : 8	58	1,885	28.7
ne 29, 30	Chinook	F	23	6.31	1 : 8	60	1,877	26.6
ly 14, 15	Sockeye	F	3	3.96	1 : 16	65	925	20.7
ly 15, 16	Sockeye	M	3	2.04	1 : 8	66	1,210	21.8
ly 24	Sockeye	F	3	5.05	1 : 8	68	1,041	28.9
ly 24, 25	Sockeye	M	3	1.46	1 : 16	68	1,319	7.8
ugust 3	Steelhead	F	4	0.63	1 : 8	66	922	13.3
ugust 7	Steelhead	M	4	0.55	1 : 16	68	693	8.4
ugust 17	Steelhead	M	5	0.15	1 : 16	68	558	19.7
ugust 18	Steelhead	F	7	0.88	1 : 16	68	757	9.8
ugust 31–September 1	Chinook	F	21	7.33	1 : 16	66	1,726	30.3
ptember 14, 15	Chinook	M	25	—[1]	1 : 16	66	1,387	—[1]
ptember 17	Chinook	M	6	—[1]	1 : 8	66	924	—[1]
ptember 21, 22	Chinook	M	5	—[1]	1 : 8	64	1,061	—[1]

[1] Fish released. No samples taken. External features of all fish indicated they were approaching sexual maturity.

eriments were made with spring- and fall-run inook salmon (*Oncorhynchus tshawytscha*), ith sockeye salmon, and with steelhead trout *Salmo gairdneri*). The results are shown in able 1. All 14 fish were actively ascending the time the tests were discontinued. There no reason to believe that most of these fish uld not have equaled or even exceeded the rformance of the original sockeye salmon. ne single sockeye tested in 1958 required 377 minutes to ascend the first 1,000 feet. ne four sockeye salmon tested in 1959 were tually faster (Table 1) in both fishways.

Throughout the 1,000-pool ascent a general crease in the hourly rate of ascent similar to e pattern of the initial day of the 1958 test uly 1, Figure 4) was discernible for all fish. ood-lactate levels of the fish that had asnded 1,000 feet (Table 1) were either equal or less than the mean blood-lactate levels fish that had been tested with ascents of ly 104 feet during 1959 (Table 2).

The abrasions that were so conspicuous on e single sockeye salmon that had ascended 648 feet were not in evidence on the fish at made 1,000-pool ascents in 1959.

DISCUSSION

Considering the apparent ease with which e 15 fish in these experiments made ascents 1,000 feet, and the absence of any evidence fatigue either in the performance of the sh or in the blood-lactate levels, it would apar that the ascent of a properly designed ool-and-overfall fishway is only a moderate ercise for chinook salmon, sockeye salmon, d steelhead trout.

The long ascents were made at two different fishway slopes, under a variety of pool hydraulic conditions, with differences in weir crests and turn pool design, and with water temperature that ranged from 58° to 68° F. Despite this, all groups were successful and rates of ascent for 1,000 feet seemed to be characteristic for each species, conforming to the pattern noted in studies of rates of ascent for 6 feet (Elling, 1960). Steelhead trout were the fastest in ascent and chinook salmon were slower than sockeye salmon.

Concern has been expressed (Andrew and Geen, 1960) that fish that fail to complete a long fishway during daylight hours might migrate back downstream out of the fishway at night causing delay and possibly resulting in the complete failure of some fish to ever reach the top of the fishway. This type of behavior, however, was never observed during the tests made with endless fishways. Under the constant lighting conditions used in the experiments, rates of ascent generally were uniform throughout the 24-hour day. Whether or not

TABLE 2.—*Mean blood-lactate levels (milligrams percent) of salmonids ascending 104 pools in endless fishways with slopes of 1 on 8 and 1 on 16, 1959*[1]

Species	1-on-8 slope		1-on-16 slope	
	n	Blood lactate	*n*	Blood lactate
Chinook	33	31.9	34	30.6
Sockeye	18	42.4	18	31.2
Steelhead	35	20.8	36	20.4

[1] Progress Report No. 52 for the month of November 1959. Research on fishway problems conducted at the Fisheries-Engineering Research Laboratory at Bonneville Dam under contract No. DA-35-026-25142 with the U. S. Fish and Wildlife Service, U. S. Army Corps of Engineers, North Pacific Division, Portland, Oregon.

a diurnal pattern of movement would exist under natural light conditions is not known.

Apprehensions that the hourly rate of fish ascent might decrease in the upper end of a long fishway and result in dangerous crowding or delay appear to be without factual foundation. Similarly, the possibility of cumulative fatigue effects resulting from ascending fishways at a series of low dams seems to be remote in view of the data from the 1,000-foot ascent tests.

The experiments with the endless fishways actually did not suggest any upper limit for the height of pool-and-overfall fishways. It would seem probable, however, that economic factors would limit the use of this type of fishway to something considerably less than 1,000 feet in height. Fishways of this type several hundred feet in height would not seem to be an excessive extrapolation of our present experience with fishways approximately 100 feet high, particularly in view of the recent experimental data. Pool-and-overfall fishways up to 1,000 feet in height may be equally feasible from the standpoint of fish behavior and ability; before accepting such an extreme view, however, several factors should be considered. One of these is the effect of water temperature on the ability and willingness of fish to ascend high fishways. The experiments at the Fisheries-Engineering Research Laboratory were made within a range of relatively moderate water temperatures (58°–68° F.). The degree to which higher water temperatures or marked changes in water temperatures might affect this aspect of fish behavior should be known.

A second consideration is the possible effect of sexual maturity on the performance of fish in fishways. Paulik and DeLacy (1958) found that the swimming ability of sockeye salmon changed as the fish migrated upstream through the Columbia River and that there was a measurable decline in swimming ability as the fish neared the spawning ground. Swimming ability was measured in terms of swimming endurance in a horizontal flume at fixed water velocities. The degree to which this measure of swimming ability can be applied to the ability to ascend pool-and-overfall fishways is difficult to assess. The fish tested in the horizontal flume were compelled to swim at arbitrarily selected velocities and exhaustion occurred within a matter of minutes, whereas fish tested in the ascent of an endless fishway selected their own pace and were able to continue for days without evidence of exhaustion. Collins *et al.*[4] were unable to find any cor lation between sexual maturity and perfor ance in pool-and-overfall fishways in f chinook salmon using the weight of gona expressed as percentage of body weight as index of maturity. The success of mature f chinook salmon in completing 1,000-pool cents would appear to confirm this. More i formation on this relationship is needed, ho ever, in view of the fact that the high da proposed on the Columbia River system a largely in upper tributaries near spawni areas and that the experiments with endl fishways were made on the lower Columb River at the early stage of migration for upp river fish.

Experience with fish behavior at a wi variety of fishways on the Columbia Riv system suggests that other factors such as w ter turbidity and odors may affect the willin ness of fish to enter and to ascend fishwa These factors probably affect fish moveme generally, whether in fishways or in the riv Until their nature is understood, however, t possibility that they might have a greater fect in a long fishway should be considered.

CONCLUSIONS

The ascent of a properly designed pool-an overfall fishway is only a moderate exerci for chinook and sockeye salmon and steelhe trout. Salmonids could ascend such fishwa even if several hundred feet in height. Und certain conditions these fish will ascend fis ways continuously day and night, and for practical purposes their rate of ascent will n decrease in the upper end of a long fishwa Fatigue effects from the fishways of a seri of low dams such as those on the Columb River appear to be very unlikely. Pool-an overfall fishways up to 1,000 feet in heig may be practical for these salmonids, at lea from the standpoint of fish behavior a ability; however, a greater knowledge of t effects of sexual maturity, water temperatu and other water qualities upon the ability salmonids to ascend high fishways should obtained.

ACKNOWLEDGMENTS

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[4] See footnote 2.

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stants who made the blood lactate determinations.

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SHALLOW WATER RESEARCH PROGRAM OF THE BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY

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This laboratory, located on Sabine Island in Santa Rosa Sound approximately 10 miles southeast of Pensacola, is well situated for aquatic research. Nearby exist environments which range from the highly saline waters of the Gulf of Mexico through the salinity gradient of a large estuarine area which receives the outflow of a number of rivers. The staff of 12 includes 7 biologists.

A portion of the overall program is concerned with biological oceanography. The objectives are (1) to document the normal estuarine relationships on a continuing basis, these data being examined to determine

se changes which are seasonal in natur and those which may be due to
ual or longer periodic cycles, and (2) [illegible] changes in the biota re-
ting from man's activities. Studies are being made of physical change
to dredge-and-fill operations and of chemical change due to domestic,
icultural and industrial wastes. The effects of these wastes are being
ntified (1) by establishing toxity levels and (2) by measuring changes in
nkton productivity and storage of radionuclides in invertebrate fauna.

Biological features being studied and methods used to estimate their
ameters are primary productivity (plankton volumes and plankton pigments)
ting rates of sedentary organisms (fouling plates), distribution and popula-
n densities of benthic animals (dredging), distribution and population densi-
s of pelagic animals (trawling), and distribution of benthic animals rarely
nd in ordinary field samples because of severe predation (protected habi-
boxes). Hydrographic features being studied are salinity, water temper-
re, pH, and visibility index (Secchi disk).

THE OCCURRENCE OF OCEANIC COPEPODS IN THE GULF OF MAINE-GEORGES BANK AREA

By

John B. Colton, Jr., Robert F. Temple, and Kenneth A. Honey

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THE OCCURRENCE OF OCEANIC COPEPODS IN THE GULF OF MAINE-GEORGES BANK AREA

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INTRODUCTION

The encroachment of oceanic immigrants upon the endemic Atlantic boreal plankton population gives evidence of the mixture of oceanic and coastal water all along the outer edge of the continental shelf between Nova Scotia and Cape Hatteras. Records of the occurrence of oceanic zooplankton species are most numerous along the 100 fathom contour, but members of

this group have also been frequently taken close into the coast west and south of Martha's Vineyard during the summer and early fall (Wilson 1932, Bigelow and Sears 1939, Deevey 1952 and 1960). This contrasts with the situation in the Gulf of Maine and Bay of Fundy (Figure 1) where records of oceanic indicators have not only

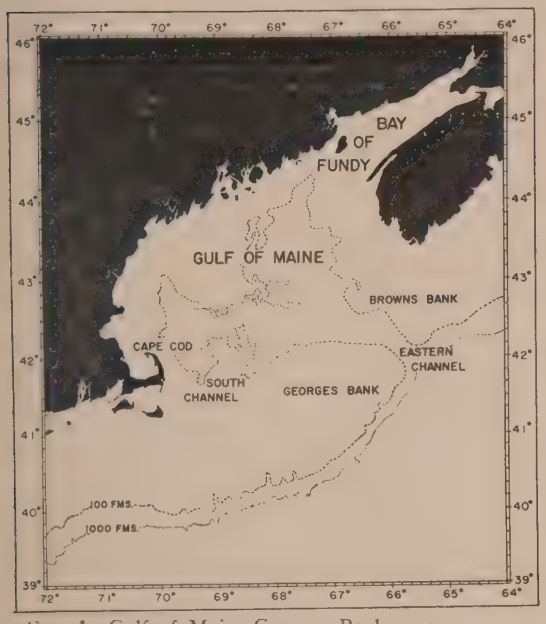

FIG. 1. Gulf of Maine-Georges Bank area.

been far less numerous than to the west of Cape Cod, but have been confined for the most part to the peripheral belt (Bigelow 1915, 1922, 1926; Fish and Johnson 1937; Legaré and MacLellan 1960). Numerous oceanic surface species may be expected along the south side of Georges Bank, but only sporadic occurrences of a few species have been reported from within the Gulf and over Georges Bank. The reason for this limited occurrence of oceanic surface species in the Gulf of Maine-Georges Bank area is that Gulf Stream and slope water seldom overflow the barrier formed by Georges Bank and that the limited surface movement into the Gulf of Maine is mostly across the eastern end of Georges Bank and via the Eastern Channel (Bigelow 1926, figure 33, p. 65).

In contrast to this usual situation many species of oceanic copepods were collected in the Gulf of Maine-Georges Bank area during the fall of 1956 and the winter of 1957. Not only is the occurrence of these exotic copepods species of interest *per se,* but also the fact that temperature conditions over the area were not unusual for this season points to the value of immigrant zooplankton species for indicating intrusions of oceanic water.

Material and Methods

The data are based on collections from U. S. Fish and Wildlife Service cruises during September, October, and November, 1956 and January, 1957. These cruises were made in the course of a cooperative investigation with the Fisheries Research Board of Canada designed to study the early life history of herring in the offshore areas of the Bay of Fundy and the Gulf of Maine (Tibbo *et al.* 1958). The sampling gear used was the Continuous Plankton Recorder (Hardy 1936) and 1-meter ring nets. The recorders were equipped with a ¾ inch square mouth opening and 60 mesh-per-inch filtering silk and were towed continuously at the surface and at 10 meters. The propellor setting was such that each 2-inch section of filtering silk represented 5 miles of tow. Fifteen-minute oblique meter-net tows (10 m to surface) were made every 4 hours. The nets were constructed of #0 silk and the towing speed was about 3 knots. Identifications and counts of zooplankton species were based on a 5% subsample of the meter net catch and a 20% subsample of each recorder section. Continuous Plankton Recorder material is based on the total catch at the surface and 10 m. Many more individuals and species were collected in the meter net than in the Continuous Plankton Recorder as the small volume of water filtered by the recorder in a 5-mile tow is not sufficient to indicate the presence of organisms in concentrations much less than 3 per m^3.

Relative Abundance and Distribution

The average number per m^3 of total copepods and oceanic copepods based on the Continuous Plankton Recorder catch during September, October, and November, 1956 and January, 1957 are presented in Table I.

TABLE I. Average abundance (number per m^3) of total copepods and oceanic copepods caught during September, October, November 1956 and January 1957

	Total Copepods	Oceanic Copepods
Silver Bay Cruise No. 1 Sept. 21-Oct. 5, 1956	393.00	1.35
Silver Bay Cruise No. 2 Oct. 15-25, 1956	257.47	0.82
Silver Bay Cruise No. 4 Nov. 14-30, 1956	148.81	1.45
Delaware Cruise No. 57-1 Jan. 28-Feb. 4, 1957	29.15	0.03

The total copepod population decreased markedly between September and February and oceanic copepods made up only a small fraction of the total copepod population during any of the cruises.

The frequency of occurrence and order of abundance of oceanic copepods caught during September, October, and November, 1956, and January, 1957 are shown in Table II.

The relative frequency of occurrence of the various species did not vary makedly between cruises, although the numbers of species caught decreased as the year progressed. Typically, the order of abundance of the various species coincided with frequency of occurrence and *Calanus minor, Candacia armata* and *Scolecithrix danae* were the most abundant and widely distributed species. Occasionally, however, the rich night-time hauls were made of the less frequently occurring species such as *Pleuromamma gracilis* and *Pleuromamma xiphias.* In most areas endemic boreal copepods, of which *Calanus finmarchicus* is a typical species, dominated the catch, but in a few locations along the southern edge of Georges Bank single or groups of oceanic species accounted for the greater proportion of the copepods caught.

The area of coverage, the distribution of surface temperature, and the frequency of occurrence of oceanic copepod species in meter-net and Hardy Plankton tows during these cruises are shown in Figure 2.

TABLE II. Frequency of occurrence and relative abundanance of oceanic copepods caught during September, October, November 1956 and January 1957. The species are listed in the order of their frequency of occurrence. The % figures indicate relative abundance

Silver Bay Cruise No. 1 Sept. 21-Oct. 5, 1956	%	Silver Bay Cruise No. 2 Oct. 15-25, 1956	%	Silver Bay Cruise No. 4 Nov. 14-30, 1956	%	Delaware Cruise 57-1 Jan. 28-Feb. 4, 1957	%
Calanus minor	36	Calanus minor	38	Scolecithrix danae	19	Calanus minor	39
Candacia armata	22	Scolecithrix danae	13	Calanus minor	14	Candacia armata	24
Euchaeta marina	16	Undinula vulgaris	5	Candacia armata	10	Pleuromamma gracilis	35
Eucalanus attenuatus	3	Candacia armata	8	Eucalanus attenuatus	1	Eucalanus attenuatus	<1
Undinula vulgaris	5	Centropages bradyi	<1	Undinula vulgaris	1	Rhincalanus cornutus	<1
Eucalanus elongatus	<1	Eucalanus attenuatus	1	Pleuromamma gracilis	23	Pleuromamma abdominalis	<1
Pontellina plumata	<1	Pleuromamma gracilis	22	Rhincalanus cornutus	1		
Candacia pachydactyla	<1	Euchaeta marina	5	Centropages bradyi	1		
Pleuromamma gracilis	6	Candacia pachydactyla	1	Candacia pachydactyla	<1		
Rhincalanus cornutus	<1	Pontellina plumata	1	Euchaeta marina	11		
Scolecithrix danae	7	Rhincalanus cornutus	<1	Pontella plumata	1		
Pleuromamma robusta	<1	Eucalanus elongatus	2	Pleuromamma abdominalis	<1		
Calocalanus pavo	<1	Pleuromamma robusta	<1	Mecynocera clausi	3		
Centropages bradyi	<1	Pleuromamma abdominalis	1	Pleuromamma xiphias	13		
Pleuromamma abdominalis	<1	Calocalanus pavo	<1				
Pontella securifer	<1	Rhincalanus nasutus	<1				
Rhincalanus nasutus	1	Mecynocera clausi	1				
Pontella spinipes	<1						
Clausocalanus arcuicornis	<1						
Oithona plumifera	<1						
Mecynocera clausi	1						

In September oceanic copepods were found over all of Georges Bank and Browns Bank although the number of species was less over shoal water than in the deeper water along the periphery of Georges Bank. Very few oceanic copepods occurred over the deeper water of the Gulf of Maine. In October and November oceanic copepods were again found over Georges and Browns Banks, but the areas in which more than 5 species occurred in the meter net tows were principally along the southern part of Georges Bank and the southeastern part of Browns Bank. Catches along the most northerly sections in the Gulf of Maine indicate a drift of oceanic copepods into the Gulf during this period.

By January the number of species and area of occurrence of oceanic copepods was greatly reduced. No meter-net tows made during January yielded more than 5 oceanic species, and positive tows were confined principally to the southern part of Georges Bank. Oddly, the only oceanic copepods found in the recorder material during January were from a few sections obtained in the Gulf of Maine. These individuals plus those caught in the one positive meter-net tow in this area confirm the presence of limited numbers of oceanic copepods in the Gulf at this season.

Surface temperature observations were the only physical data collected during these cruises in sufficient detail to indicate an intrusion of oceanic water. However, the surface temperatures as shown by the isotherm lines plotted in Fig. 2 were not unusually high for this period of the year. Although the oceanic copepods tended to be concentrated in the warmer water areas and were not found in water much colder than 40° F, there does not appear to be a strong correlation between the area and frequency of occurrence of oceanic copepods and surface temperature as was demonstrated for tropical and oceanic fish larvae collected during these cruises (Colton 1961).

Although all the oceanic copepods collected were adults, no specimens carrying attached spermatophores or egg cases were found. Late immature stages and reproducing adults of several species of oceanic copepods have been collected in the coastal water south of Cape Hatteras (St. John 1958), but it is doubtful that any of the immigrant copepod species reproduce in the Gulf. Their continued presence, however, indicates that they are able to survive sufficiently long in boreal waters to become widely distributed. The areas in which the various copepod species were caught in meter-net and Hardy Plankton Recorder tows during September, 1956 through January, 1957 are shown in Figure 3.

Scolecithrix danae, Calanus minor, Candacia pachydactyla, and *Candacia armata* were the most widely distributed species and were found over Georges Bank, Browns Bank and southern part of the Gulf of Maine. Previous reports on the occurrence of these species in the Gulf of Maine-Georges Bank area have all been for a few specimens, although Dr. George Grice of the Woods Hole Oceanographic Institution (personal communication) reports that he sometimes finds *Candacia armata* in considerable abundance over the continental shelf south of Montauk, Long Island.

The main areas of occurrence of *Euchaeta mariana, Undinula vulgaris, Rhincalanus cornutus, Pleuromamma gracilis, Centropages bradyi, Eucalanus elongatus,* and *E. attenuatus* were over the Great South Channel between Georges Bank and Cape Cod, the Eastern Channel between Georges and Browns Banks, and the southern part of Georges Bank. The other oceanic copepod species were found principally over deep water along the southern edge of Georges Bank.

DISCUSSION

The large number of individuals and species of oceanic copepods and their wide distribution yield evidence of an intrusion of oceanic water into the Gulf of Maine-Georges Bank area. The general distribution patterns of the various species indicate that this intrusion resulted for the most part from an overflow of oceanic water across the southern edge of Georges Bank al-

FIG. 2. The distribution of surface temperature and the frequency of occurrence of oceanic copepods, September, October, November, 1956 and January, 1957.

though the distribution of species such as *Euchaeta marina* indicate that there was also an indraft via the Eastern Channel which is the usual route for such planktonic immigrations (Bigelow 1926, Redfield 1939, Redfield and Beale 1940).

Although these oceanic copepods fail to breed to an appreciable extent in boreal coastal waters and their continued presence depends on successive waves of immigration, they are able to survive under the physical conditions encountered in the Gulf of Maine for considerable periods of time. The longevity of these copepods limits their value as indicators of the time of such intrusions of oceanic water. In this instance however, we have additional information which allows us to approximate this time. Drift bottles released during February, March, April, May and June, 1956 (Day 1958, Colton and Temple 1961) and during the cruises under discussion (Colton and Temple 1961) showed no evidence of any water movement across Georges Bank from south to north, although a few bottles released over the southwestern part of Georges Bank drifted northwesterly toward the offing of Martha's Vineyard in May and June. It appears, therefore, that this overflow of oceanic water took place sometime in July or August which is the time such intrusions have frequently been observed west and south of Martha's Vineyard (Bigelow 1926, Bigelow and Sears 1939, Redfield and Beale 1940, Deevey 1952).

That similar large-scale intrusions of oceanic immigrants into the Gulf of Maine-Georges Bank area have not been witnessed previously may be due in part to the infrequency of coverage of this area during late summer and early fall when wind and hydrographic conditions are most conducive to a breakdown of the normal density barriers existing between coastal and oceanic water. Such overflows of oceanic water would tend to counteract the general offshore movement of surface water from Georges Bank. It has been postulated by Colton and Temple (1961) that the year class strength of many commercial fish species inhabiting Georges Bank is regulated in part by the magnitude and frequency of this offshore drift. Additional surveys during late summer and early fall designed to obtain detailed information on the frequency and the physical and biological effect of such intrusions are warranted.

SUMMARY

Twenty-two species of oceanic copepods were collected in the surface waters over the Gulf of Maine and Georges

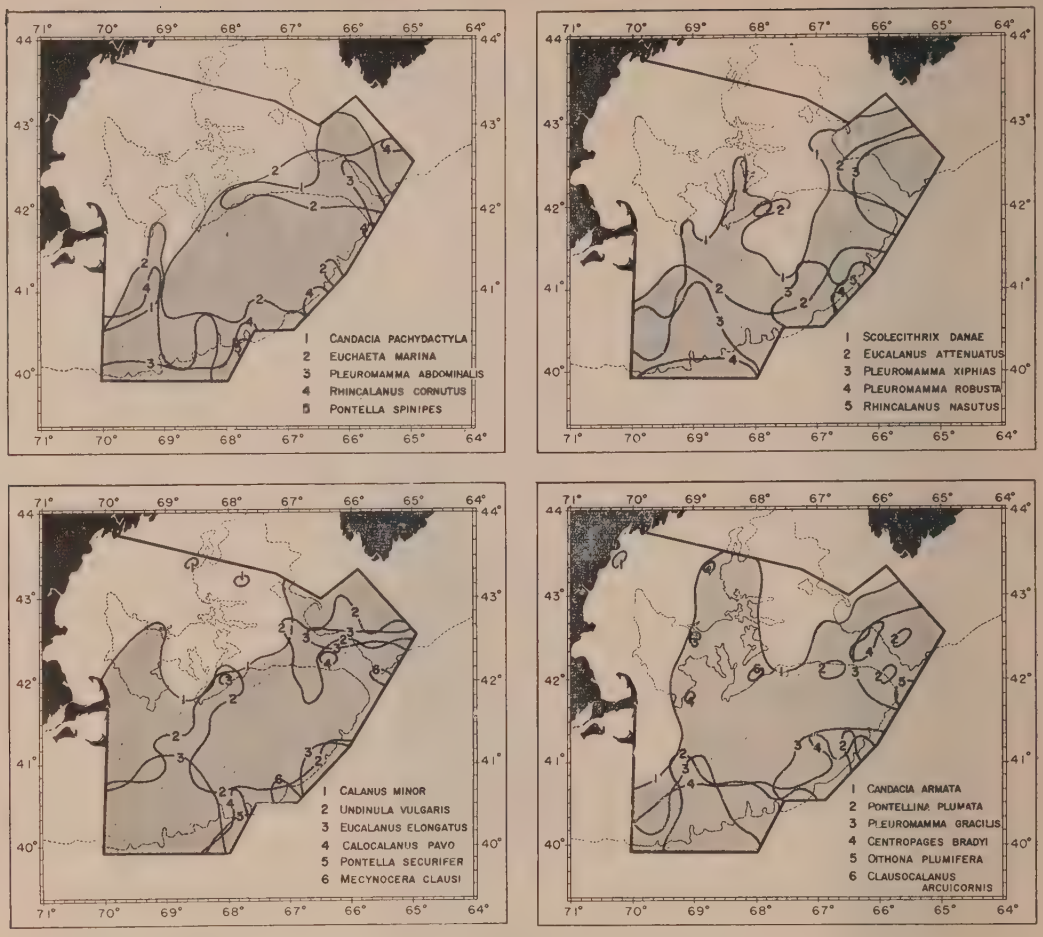

FIG. 3. Distribution of oceanic copepods, September, 1956-January, 1957.

Bank during September, October, November, 1956 and January, 1957. Only sporadic occurrences of a few species of oceanic copepods have been reported previously from this area and these records have been confined for the most part to the peripheral belt. Although surface temperatures were not unusually high for this period of the year, the distribution and abundance of the various copepod species yield direct evidence of an intrusion of oceanic water across the southern edge of Georges Bank and into the Gulf of Maine. Indications are that this overflow of oceanic water took place sometime in July and August. Since such intrusions would tend to counteract the general offshore movement of surface water from Georges Bank, the magnitude and frequency of which have been postulated to regulate in part the year class strength of many commercial fish species inhabiting Georges Bank, additional observations as to the occurrence of oceanic indicator species are warranted.

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USE OF THE HARDY CONTINUOUS PLANKTON RECORDER IN A FISHERY RESEARCH PROGRAMME

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INTRODUCTION.

THE abundance of haddock on Georges Bank, like that of most great fish stocks, is subject to considerable variation. These fluctuations are the result of strong differences in the strengths of year classes from year to year. Knowledge regarding the causes of these differences in year-class strength is necessary to an understanding of the biology of the haddock and is required for forecasting future abundance of the species.

Walford (1938) postulated that weak year classes of Georges Bank haddock result from the drift of larvae beyond the area in which they can survive. According to this theory the eggs and larvae from the spawning on the northern edge of the Bank normally drift around the Bank clockwise in the Georges Bank eddy. Under certain conditions the circulation might be displaced to the south carrying the larvae beyond their normal habitat and into waters inimical to their survival.

Walford studied the distribution of eggs and larvae on the Bank in the years 1931 and 1932. On the basis of some differences in the distribution of larvae in the two years he suggested a difference in the strength of the two year classes. Records of commercial landings later showed that both the 1931 and the 1932 year classes were weak ones. Walford's results were inconclusive and his hypothesis not adequately tested.

Accordingly, a plan was developed to make another attempt to relate the drift of larvae to the survival of the year class as expressed in landings of fish in the commercial catch. The principal problem presented was to locate the egg concentrations and follow them as they drifted with the currents. It was hoped that the water masses containing the developing larvae could be followed and the fate of the fish observed directly until they began to descend to the bottom to take up their ultimate demersal life.

Since all the spawning populations which might contribute to the Georges Bank stock are not known, it was necessary to plan plankton surveys covering all of the Gulf of Maine and Georges Bank in order to assure finding all the significant concentrations of eggs and to follow their drift over the entire region. It was further required that the entire area be covered in less than a month's time.

The Hardy Continuous Plankton Recorder was selected as the only available instrument which could cover the area in the required time and give a continuous record of the plankton. With this instrument the area could be traversed at the full cruising speed of the vessel. The speed and endurance of the ship were the only limitations on the extent of the area covered.

Since Plankton Recorders have not been employed previously on research vessels, this report is written to illustrate their applicability in a general plankton research programme.

The Continuous Plankton Recorder was described in detail by Hardy (1936, 1939). Briefly, it is an instrument which can be towed at high speed for many hours without attention. Water enters a small opening in the nose of the Recorder and is filtered through a moving band of silk gauze, providing a continuous sample of the plankton taken along the entire course of the vessel. The grade of filtering silk used for this study was 60 meshes per inch. The amount of water filtered is directly proportional to the size of the entrance aperture if the aperture is $\frac{3}{4}$-inch square or less (Hardy, 1936, 1939). The quantity of plankton collected on a unit length of silk gauze can be expressed in terms of distance towed or volume of water strained.

Methods.

Surveys were made in March, April and May of 1953; February, March, April and May of 1955; February, March, April, May and June of 1956. One Recorder was towed just below the surface from a boom on the forward quarter and another, simultaneously, at a depth of 10 metres from a boom located at the after gallows frame. Both recorders were towed from the starboard side of the vessel. A speed of 10 knots was maintained by the vessel while the instruments were under tow.

Additional observations included bathythermograph lowerings (hourly), wind observations and surface water samples for salinity determination (every 2 hours), drift-bottle releases at selected stations, and surface plankton samples with a one-metre net (every 12 hours).

A portion of the fish eggs from the net sample was preserved and the rest used for hatching on board ship. This latter procedure was necessary for the determination of the ratio of cod eggs to haddock eggs since the two species could not be distinguished in the early egg stages. The ratio of cod to haddock for the net station was used to estimate the identity of the eggs on the applicable part of the recorder silk.[1]

Validity of the Recorder Sample.

The Recorder was developed for use on commercial vessels and has proved to be an adequate instrument for " roughing out " the general patterns of plankton distributions in the areas of study. Since phytoplankton and zooplankton populations are subject to large fluctuations in local abundance, a precise count is not required to record the rise and fall of populations as they drift with the currents. That the interrelationship of species within the community and their relations to hydrographic factors can be elucidated from the kind of sampling which the Recorder provides has been amply demonstrated by Hardy (1939), Lucas (1940), and Rae and Fraser (1941).

In our study of the drift of haddock eggs and larvae, we did not attempt a census but rather endeavoured to " keep track " of the concentrations until their ultimate fate was determined. We wondered, however, whether the concentration of eggs and larvae as expressed by numbers per cubic metre bore any relation to the concentrations indicated by other sampling methods. No experiment was set up to make this comparison ; the metre-net tows during these cruises were not standardized as they were designed solely for the purpose of obtaining eggs for hatching and identification. A general idea of the adequacy of the Recorder sample can be obtained, however, by comparing our results with collections made by other workers in the area who used other collecting devices. For example, a comparison of our samples, taken with a Recorder, with those of Walford (1938), who used one-metre nets in 1931 and 1932, indicates that the results are at least of the same order of magnitude (Table I). No better agreement could be expected considering the differences which occur in the concentrations of eggs in the water from year to year.

In considering the possible avoidance of collecting gear we are fortunate to have at hand data collected by G. L. Clarke and D. F. Bumpus on Georges Bank during the springs of 1940 and 1941. These collections were made with a Clarke-Bumpus Plankton Sampler (Clarke and Bumpus, 1940) towed at a speed of two knots in two or three oblique hauls to a maximum depth of 200 metres. The distribution of *Sagitta elegans* in their collections has already been reported (Clarke, Pierce, and Bumpus, 1943). All other zooplankton data based on counts made by Bumpus and Pierce have been placed at our disposal by Dr. Clarke.

An analysis of these data showed that the size range of haddock and cod larvae caught during these cruises was considerably smaller than that of haddock and

[1] Details regarding the methods of collection and analysis of data during these surveys are to be given in a subsequent report.

TABLE I.—*Recorder Samples and One-metre Ring Net Samples Compared. Haddock and Cod Eggs per Cubic Metre of Water.*

Walford (1938)* :

One-metre net, March–June 1931 and 1932, Georges Bank.

Table 4	.	0·451
Table 5	.	0·034
Average	.	0·243

Continuous Plankton Recorder :

March–May 1953, February–May 1955 and 1956, Gulf of Maine—Georges Bank.

Cruise No.	Date.	Surface.	10 meters.	Average.
Albatross 46	March 1953	0·251	0·072	0·162
Albatross 48	April 1953	0·080	0·039	0·060
Albatross 50	May 1953	0·002	0·000	0·001
Average		0·111	0·037	0·074
Albatross 57	Feb. 1955	0·174	0·057	0·116
Albatross 58	March 1955	0·223	0·048	0·136
Albatross 60	April 1955	0·245	0·045	0·145
Albatross 61	May 1955	0·027	0·007	0·017
Average		0·167	0·039	0·103
Albatross 71	Feb. 1956	0·120	0·112	0·116
Albatross 72	March 1956	0·303	0·311	0·307
Albatross 73	April 1956	0·451	0·250	0·351
Albatross 75	May 1956	0·042	0·023	0·033
Average		0·229	0·174	0·202

* From Walford's Tables 4 and 5, pp. 64 and 65. His values of eggs per minute converted to eggs per cubic metre. His data for upper levels only used here (approximately upper 50 metres).

cod larvae caught by the Plankton Recorder at the same season during 1953, 1955, and 1956 (Table III). This undersampling appears to be due to avoidance, since the whole water column was sampled, and even with the smaller sizes represented, more larval fish of all species were caught with the Clarke-Bumpus Sampler during the night hauls than during the day hauls at all depths. There was no consistent diurnal difference in the average number of larval haddock and cod caught in the Recorder although there was a slight increase in the average length of larvae taken at night during most cruises (Table II).

TABLE II.—*Average Length and Number per Cubic Metre of Haddock and Cod Larvae Caught During the Day and Night on Recorder Surveys of* 1953, 1955 *and* 1956.

Day.			Night.	
Number.	Length (mm.)		Number	Length (mm.)
0·019	8·3	.	0·019	10·1

Efficiency of Capture.

The catching power of the Recorder depends upon the size of the sampling aperture and of the water tunnel, the speed of tow, and the grade of silk used. To prevent clogging, the sampling aperture must be small compared with the cross-section area of the water tunnel where the filtering gauze crosses it. The standard size openings are $\frac{1}{2}$ inch square and $\frac{3}{4}$ inch square. The ratios of gauze area to sampling aperture are 32 to 1 and 13 to 1 respectively. These ratios of filtration area to aperture are much larger than in an ordinary tow net, thus assuring a more rapid movement of water through the mouth of the gear. This results in more efficient capture of organisms capable of performing avoidance reactions to the oncoming collecting mechanism.

Fish and eggs larvae.

The Hardy Plankton Recorder is probably more effective in capturing fish larvae than the Clarke-Bumpus Sampler or the one-metre net. Ahlstrom (1954) has demonstrated undersampling of sardine larvae in daytime hauls and an increase in undersampling with increase in size of fish ; he based his observations on oblique one-metre net tows. Since his sampling extended below the depth limits frequented by sardine larvae, Ahlstrom concluded that the undersampling during daylight hours was due to avoidance rather than to diurnal migrations. The avoidance of ring nets by larger larvae has been noted for other species of fish as well (see Bridger, 1956) and may also occur to a limited extent during the night.

Larger larvae avoid the collecting gear more effectively than the smaller larvae. This was demonstrated by Ahlstrom (1954) and Bridger (1956) and is evident in the collections of Clarke, *et al.*, when compared with our Hardy Recorder data. In Table III we compare the lengths of larvae taken with each kind of gear, arranged by dates. The Clarke-Bumpus collections were made on seven cruises in April, May and June of 1940 and 1941. The average lengths of larvae for each of the seven cruises is smaller than the averages for the Plankton Recorder collections made in the same months of 1953, 1955 and 1956. The upper limit of sizes is very much greater in the case of the Recorder data, reaching as high as 40 mm., whereas the maximum size taken with the Clarke-Bumpus sampler was 11 mm. In the case of the Recorder material there is a fairly regular increase in both the average size and the maximum size of larvae taken from March to June in all three years whereas in the Clarke-Bumpus samples the increase in size with time is very slight. Evidently the Clarke-Bumpus Sampler undersamples the larger larvae.

A further indication of the efficiency of the Plankton Recorder is shown by a comparison of sizes of larvae taken with it and with our own metre net on the same cruises. In Table IV it will be seen that the average size and the range in size of haddock and cod larvae taken in the Hardy Plankton Recorder were comparable to those collected in the one-metre net surface tows. These data are for all surface samples taken during the three years of observation.

TABLE III.—*Comparison of Sizes of Haddock and Cod Larvae Taken with Two Kinds of Collectors.*

Clarke-Bumpus Sampler.				Hardy Plankton Recorder.			
Date.	Cruise No.	Average size (mm.).	Range in size (mm.).	Date.	Cruise No.	Average size (mm.).	Range in size (mm.).
1940				1953			
April	96	4·8	3·0–10·0	March	46	4·6	4·0–5·0
May	97	4·5	3·0–8·0	April–May	48	8·0	4·5–15·0
June	98	4·5	3·0–10·0	May–June	50	19·6	6·5–35·0
June	100	6·4	3·0–10·0	1955			
1941				Feb.–March	57	4·8	3·7–5·5
April	113	3·5	3·0–4·0	March	58	6·0	3·7–10·0
May	114	4·2	3·0–10·0	April–May	60	8·1	4·5–18·0
June	116	5·8	3·0–11·0	May	61	8·5	3·8–20·0
				1956			
				Feb.–March	71	4·0	3·1–4·9
				March	72	4·6	3·3–8·0
				April	73	5·4	3·5–10·0
				May	75	7·0	3·1–28·0
				June	76	24·8	12·0–40·0

TABLE IV.—*Comparisons of Size of Haddock and Cod Larvae Collected in* 1953, 1955 *and* 1956.

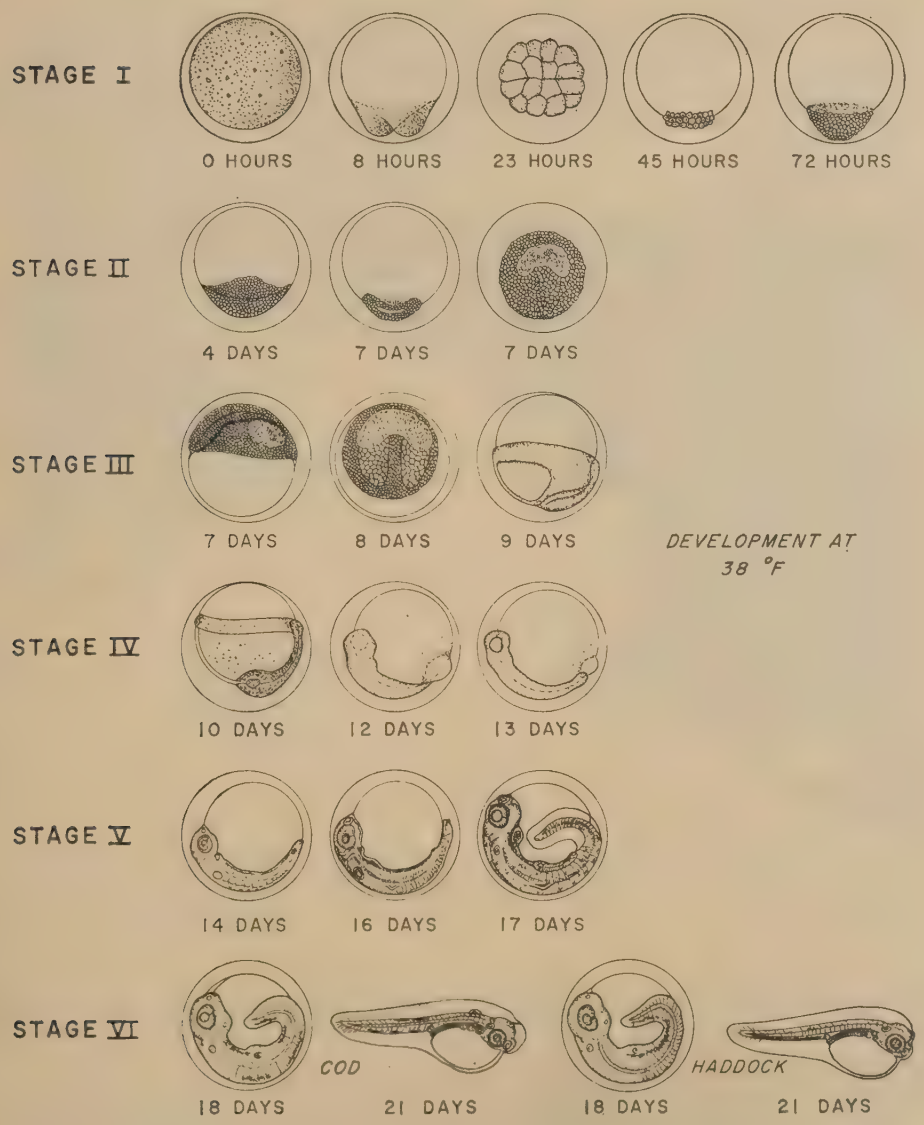
	Average size (mm.).	Range in size (mm.).
Continuous Plankton Recorder .	8·5	3·1–40·0
One-metre net	7·4	3·0–29·0

One of the distinct advantages of the Plankton Recorder lies in the size of area that can be covered in a given amount of time. As pointed out above, the only limit is the speed and endurance of the ship used. Since the currents are fairly rapid in our area and the exact spawning sites not well known, our early cruises were designed to cover the Gulf of Maine, Browns Bank, and Georges Bank (see Text-fig. 5) in as short time as possible. Some results of the cruises of 1953 will be presented here as an example of the kind of coverage that can be accomplished with the Plankton Recorder.

Three plankton-hydrographic cruises were made in the spring of 1953. The first was "Albatross III" Cruise 46 in March and April when 2,354 miles were covered in 15 days. On the next, Cruise 48, 3,027 miles were covered in 15 days ; and on the third, Cruise 50, 1,856 miles were covered in 10 days.

For determining the relative age of cod and haddock eggs six stages were recognized as follows (see also Text-fig. 1):

Stage I.—From fertilization to the formation of the early blastodermal cap.
Stage II.—From the completed blastodermal cap to the development of the segmentation cavity.



TEXT-FIG. 1.—The six developmental stages of cod and haddock eggs.

Stage III.—From the appearance of the early embryonic axis to the approach of the germinal ring to an equatorial position.

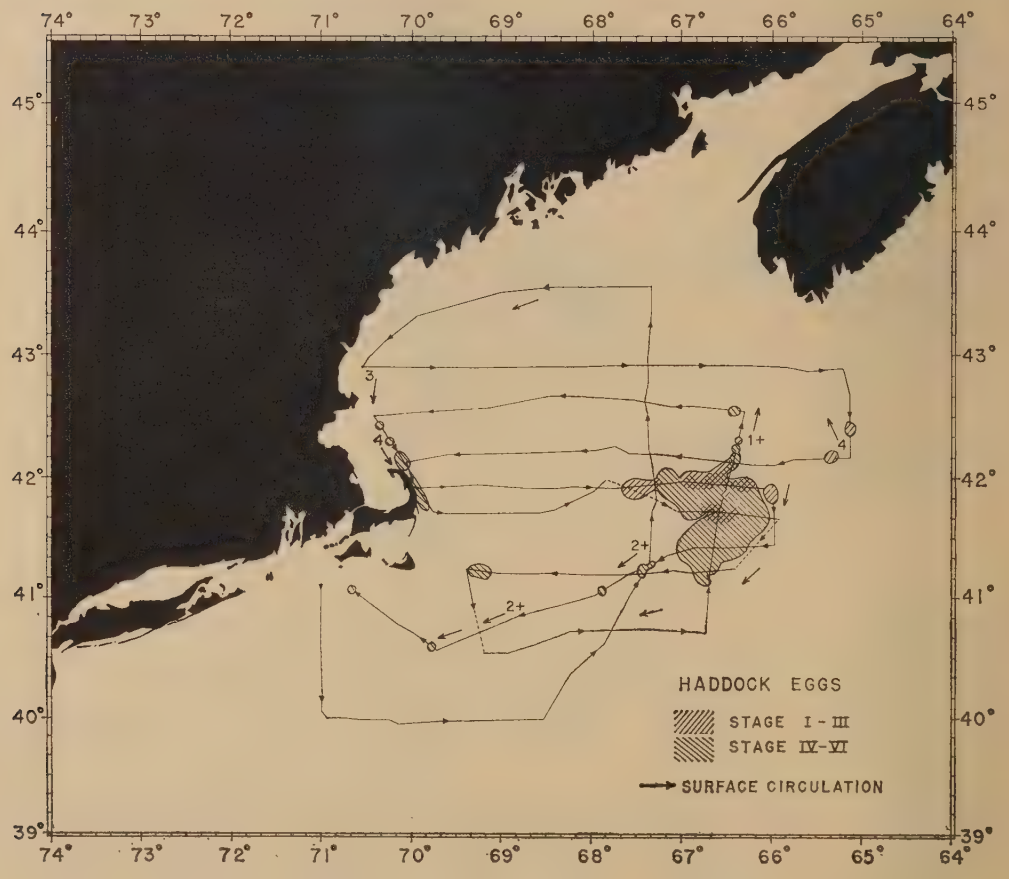
Stage IV.—From the equatorial position of the germinal ring to just before blastopore closure.

Stage V.—From blastopore closure (half circle) to almost full circle (scattered pigmentation).

Stage VI.—From the formation of the characteristic pigment pattern to hatching.

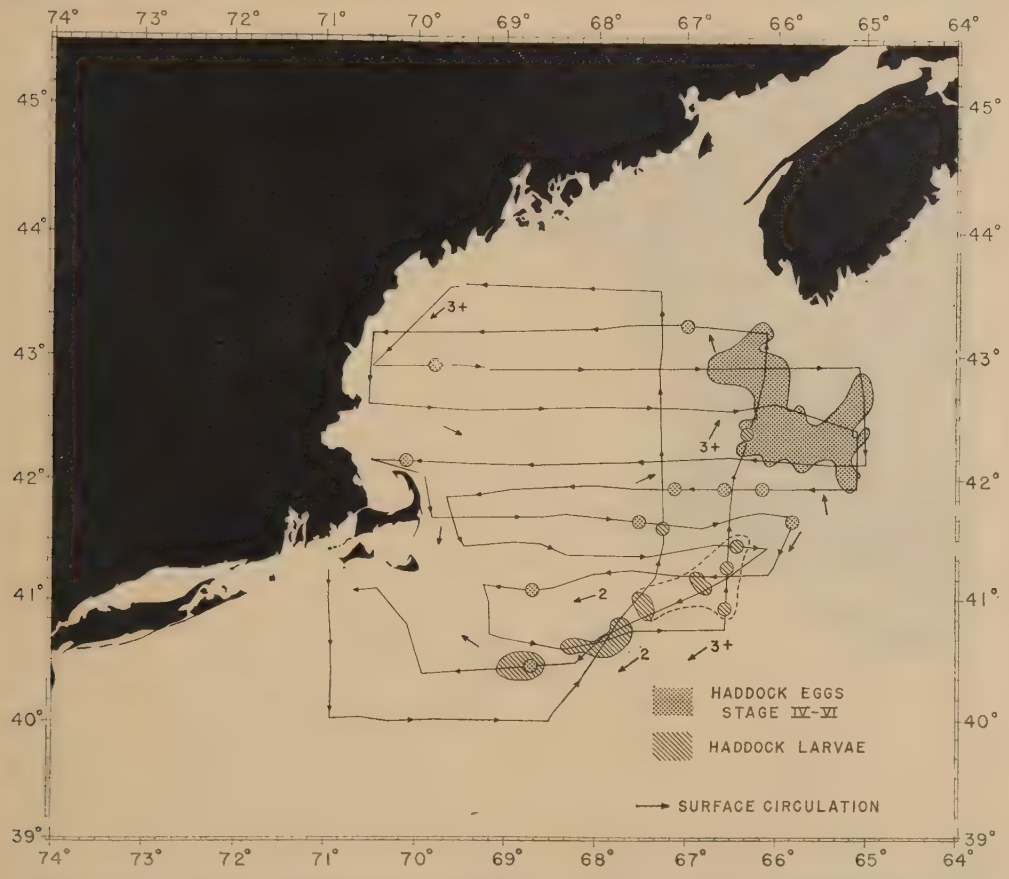
The two species usually cannot be distinguished until stage VI.

A large concentration of haddock eggs was found on the first cruise in March and its area was delimited (Text-fig. 2). Larvae assumed to have hatched from these



TEXT-FIG. 2.—Track of Continuous Plankton Recorder, locations of haddock eggs (from surface and 10-metre Recorders), and speed and direction of surface circulation, March 19–April 2, 1953. The speed of surface currents is shown, in Text-figs. 2, 3 and 4, in miles per day (from Day, 1958).

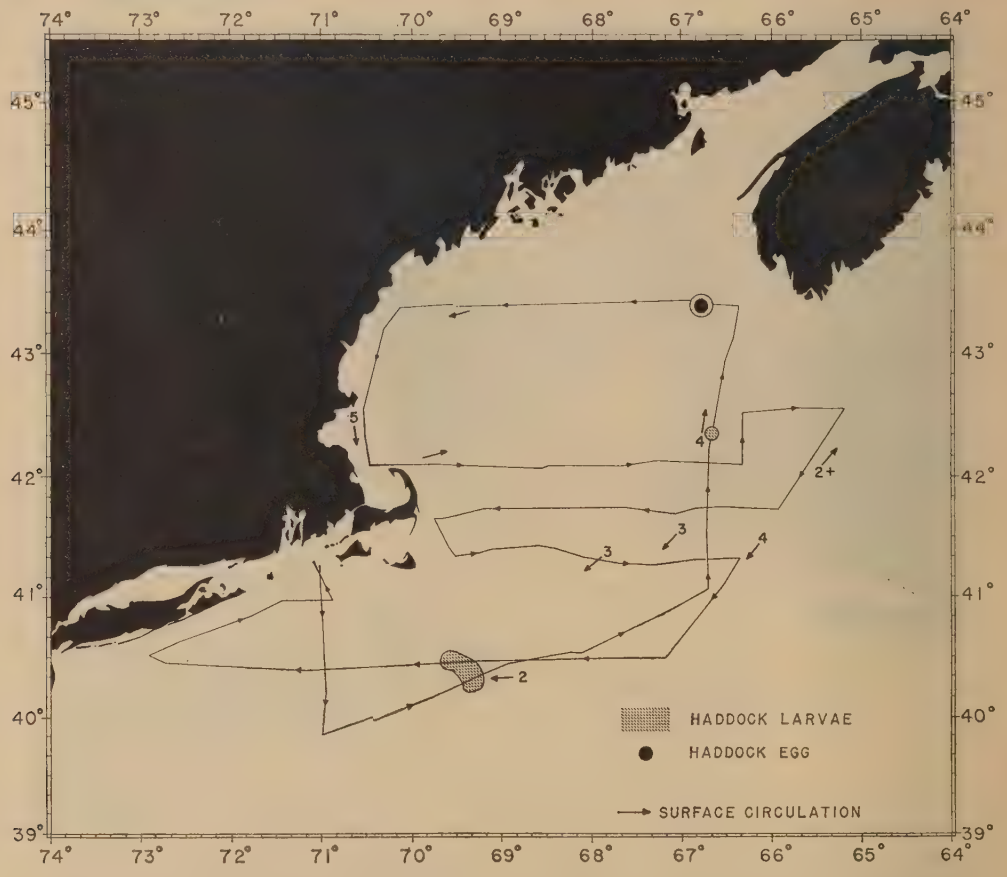
eggs were picked up on the second cruise (Text-fig. 3) and again on the third cruise (Text-fig. 4). Drift of the eggs and larvae and growth of the larvae were determined from the observations of these three cruises. A large concentration of eggs was found on Browns Bank on the second cruise and some indication of it was found on the third cruise.



TEXT-FIG. 3.—Track of Continuous Plankton Recorder, locations of haddock eggs and larvae (from surface and 10-metre Recorders), and speed and direction of surface circulation, April 24–May 8, 1953.

Text-fig. 2 shows the distribution of haddock eggs as found on the first cruise which extended from March 19th to April 2nd, 1953. All stages of haddock eggs were found, but early stages were confined for the most part to the northern edge of Georges Bank, a known spawning locality and probably the most important ground for the Georges Bank stock. The later-stage eggs were found in a large area which included the northern edge but extended 45 miles to the south.

Analysis of drift-bottle returns indicates currents to the south and west in the spawning area. Thus, the eggs would be expected to drift to the south-westward. On the following cruise (April 24th–May 8th) larvae were, indeed, found in the area to the south-westward of the spawning area (Text-fig. 3). The larvae extended in a line from the southern part of the area where eggs were found on the previous



TEXT-FIG. 4.—Track of Continuous Plankton Recorder, locations of haddock and an egg larvae (from surface and 10-metre Recorders), and speed and direction of surface circulation, May 25–June 3, 1953.

cruise to a point 120 miles to the south-westward. The larvae could be divided into a north-eastern group with a mean length of 5·5 mm. and a south-western group with a mean length of 6·4 mm. If the 5·5 mm. group is assumed to represent the early-stage eggs found on the previous cruise, the larvae had grown an average of 0·053 mm. per day. Likewise, if the 6·4 mm. group is assumed to represent the late-stage eggs found on the previous cruise, these larvae grew an average of 0·063 mm. per day. These growth increments agree well with the estimates of Bigelow

and Welsh (1925) and Walford (1938). The temperature of the water is important in this connection. Surface temperatures in the area of eggs on the first cruise averaged 41·4° F. These temperatures are compatible with the growth estimated for the larvae found.

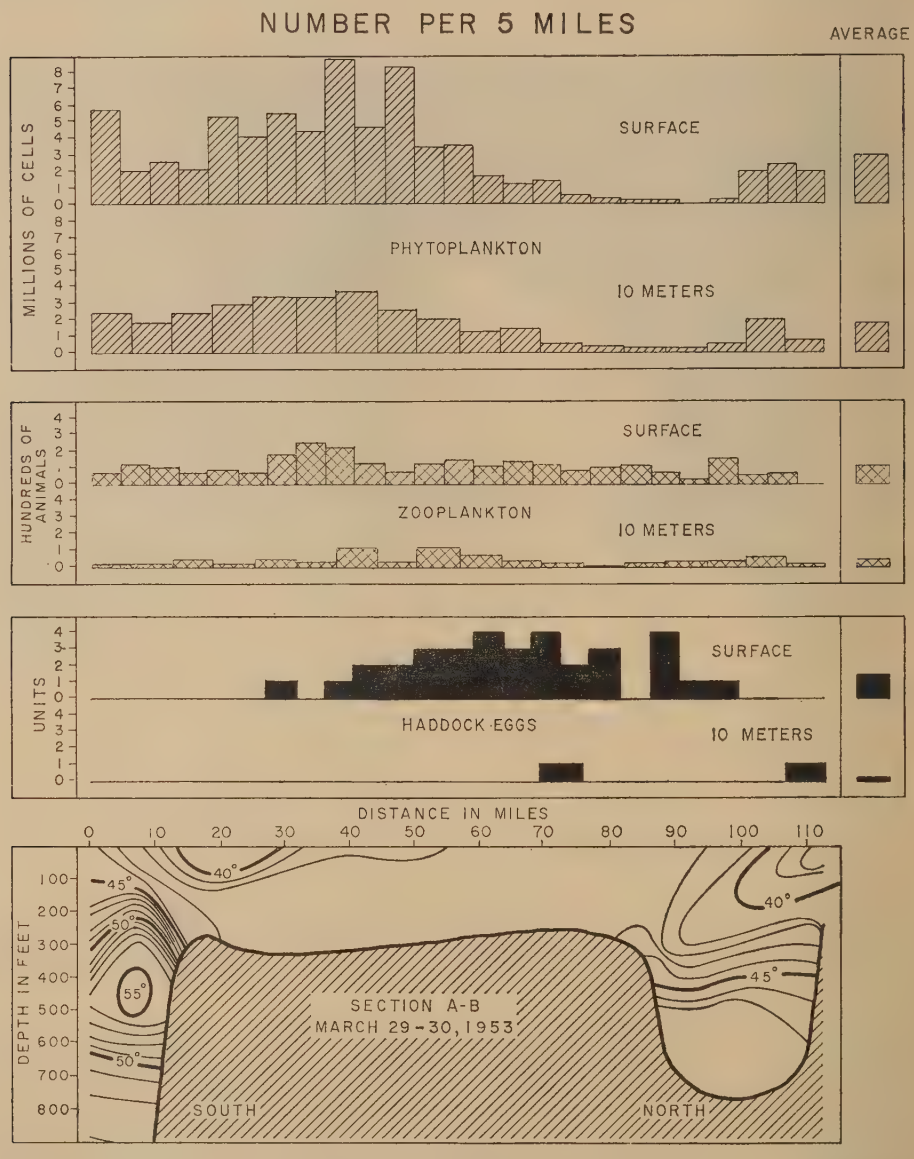
The distance of drift indicated by these studies is corroborated by estimates of drift determined by other methods. The position of the 5·5 mm. larvae indicates a

Text-fig. 5.—Location of Section A–B, Georges Bank, March 1953.

drift of 3·5 miles per day while the position of the 6·4 mm. larvae indicates 4·0 miles per day. These velocities agree with those computed by Day (1958) on the basis of drift bottles released on these same cruises and with velocities generally known to occur in the area (Bigelow, 1928).

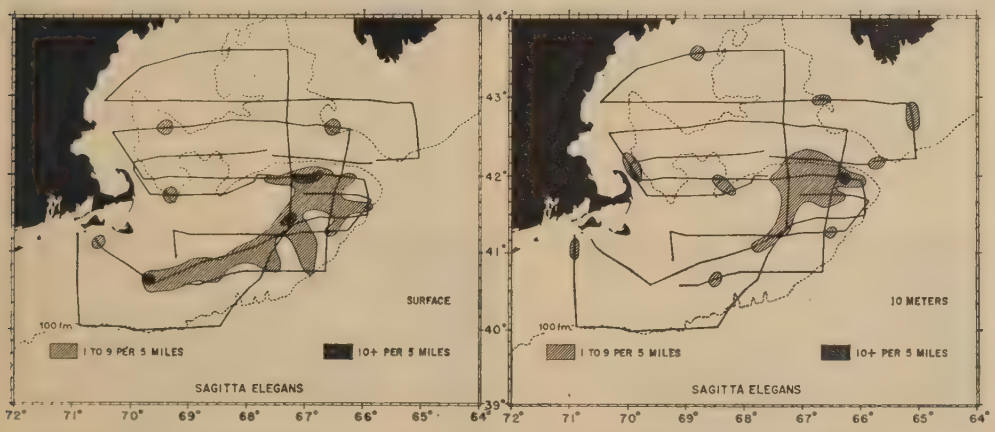
On the third cruise only one small patch of haddock larvae which could be identified as the result of Georges Bank spawning was found (Text-fig. 4). These averaged 21 mm. in length. From the knowledge we have on growth rates (Walford, 1938. Dannevig, 1919) and the non-tidal drift at this time of year, it is deduced that this group represented the 6·4 mm. larvae found on the previous cruise. The calculated daily growth increment was 0·52 mm. and the drift velocity 1·6 miles per day.

Practically no haddock eggs were found on Browns Bank until the second cruise (Cruise No. 48). At this time a large group of eggs, all in late stages of development, was found covering a wide area of the Bank (Text-fig. 3). These were collected from April 28th to May 6th.



TEXT-FIG. 6.—Numbers per 5 miles of all phytoplankton, zooplankton, and haddock eggs at the surface and 10 metres, March 1953, Section A–B (see Text-fig. 5).

On the next cruise this area was traversed from May 27th to May 30th. The concentration of eggs had disappeared. The only larva found that could be associated with the Browns Bank spawning was one specimen (Text-fig. 4) having a length of 6·5 mm. and located to the northwestward of the Bank. The main body of eggs had either succumbed to vicissitudes of nature or drifted out of the area surveyed during the second cruise. The one larva found would indicate a drift of about 3·0 miles per day which is less than indicated by drift bottles released in the area. These showed a drift of 4·0 miles per day toward the north. Perhaps the rest of the Browns Bank larvae drifted at 4·0 miles per day or faster and were carried up into the Bay of Fundy by late May, the time of this second cruise.



TEXT-FIG. 7.—The distribution of *Sagitta elegans* at the surface and 10 metres, March, 1953.

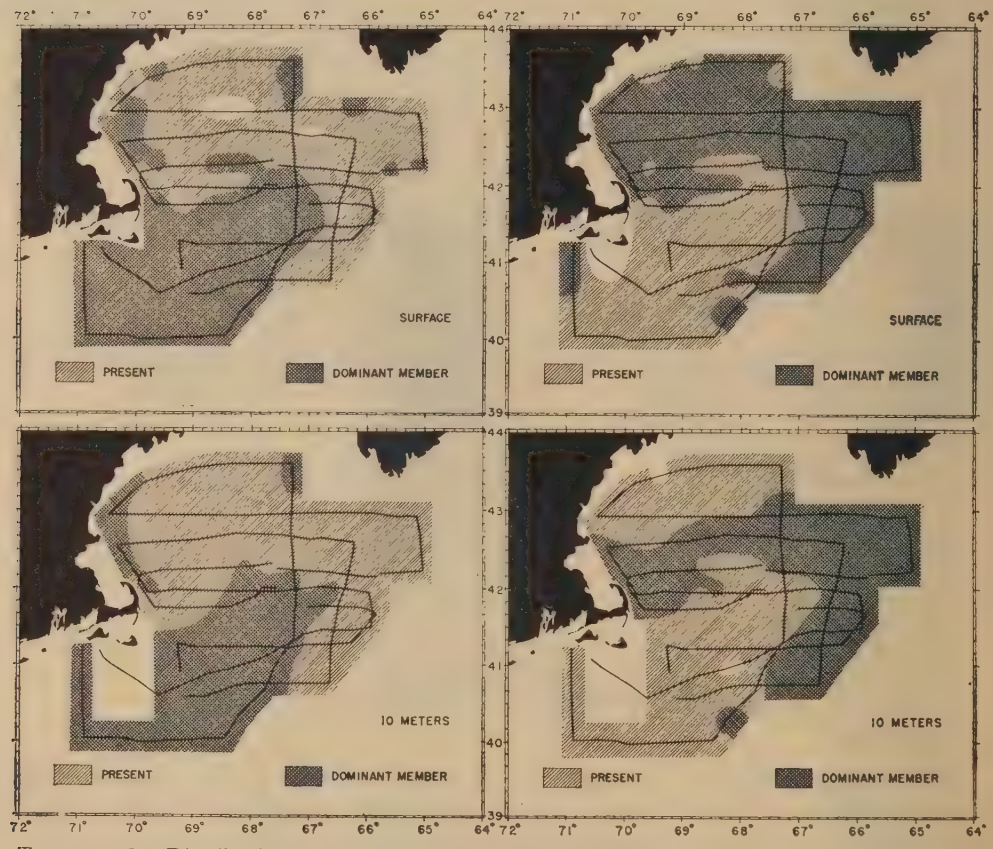
Other plankton.

It has been concluded by Hardy (1939) and Rae and Fraser (1941) that, if a proper mesh size is selected, the Continuous Plankton Recorder obtains a reliable sample of most species of fish eggs, fish larvae and other zooplankton, and that the catches compare both quantitatively and qualitatively with those of any other type of gear. In our studies a mesh size of 60 threads to the inch was used throughout (the same as that used by Hardy and by Rae and Fraser) with an approximate aperture size of 0·3 mm. Lucas (1940), showed that silk of this mesh size provides a surprisingly useful Recorder sample of the larger phytoplankton species, sufficient to delimit the areas of abundance of such forms. We found this to be true in our collections as well.

A comparison of the Plankton Recorder catches at the surface and 10 metres is made for a north-south section across the eastern part of Georges Bank in late March 1953 (Text-figs. 5 and 6). It will be noted that the haddock eggs were found almost exclusively at the surface rather than in the 10-metre tows and that they were found almost exclusively in water temperatures between 40° and 43° F.

Zooplankton was abundant throughout the section but phytoplankton was concentrated in the central and southern parts of the Bank.

Recorder information is also useful in delimiting different water masses on the basis of occurrence of indicator species. Clarke, Pierce and Bumpus (1943) showed

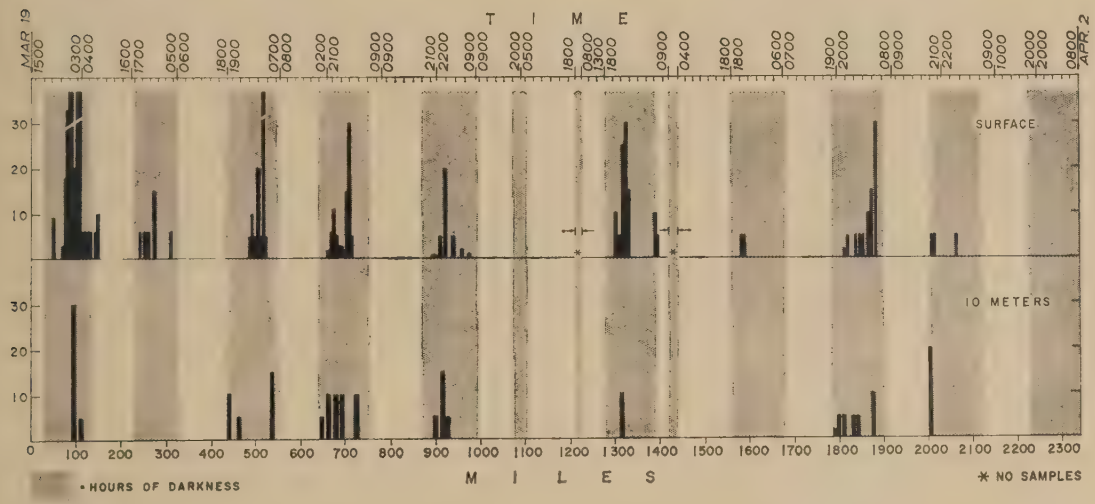


TEXT-FIG. 8.—Distribution of *Thalassionema nitzschioides* (left) and *Thalassiosira nordenskioldii* (right) at the surface and 10 metres, March 1953.

that *Sagitta elegans* was characteristic of Georges Bank water and was not found to any extent in Gulf of Maine water. Our Recorder data corroborates this and clearly delimits the occurrence of *S. elegans* on Georges Bank in March 1953 (Text-fig. 7).

Two species of diatoms, *Thalassionema nitzschioides* and *Thalassiosira nordenskioldii*, promise to be indicators of Georges Bank water and Gulf of Maine water. The dominances of their occurrences were reciprocal (Text-fig. 8). Without recourse to precise counting, the relative abundance of these species could be determined quickly from Recorder silks. Such observations could be very useful in helping to identify water masses in the area.

Another advantage of continuous sampling with the Hardy Plankton Recorder is the clarity with which the vertical migratory patterns of some animals showed up when plotted with respect to time and depth. Text-fig. 9 shows the distribution of *Metridia lucens*, at the surface and at 10 metres along the whole course of the March-April 1953 cruise.



TEXT-FIG. 9.—Distribution of *Metridia lucens*, at the surface and 10 metres during the day and night, March 19–April 2, 1953. The histograms and the scale at left show the number of *Metridia* per five miles of Recorder tow.

CONCLUSIONS.

The Continuous Plankton Recorder is a useful tool in a fishery research programme. Although it has certain limitations, these are outweighed by a number of advantages over other collecting mechanisms.

Disadvantages include smallness of sample. The number of fish larvae collected at a particular station, for instance, may be so small as to preclude estimations of abundance having any statistical validity. Samples from other collecting devices also suffer from this inadequacy but to a lesser extent.

The Recorder has a tendency to crush larger specimens against the gauze and in some instances distort them beyond recognition. As one becomes accustomed to working with Recorder material one learns to identify specimens in this condition.

It is the authors' opinion that the above disadvantages are far outweighed by the Recorder's ability to fish continuously at the full speed of the vessel even in rough weather, and at 2 levels simultaneously (it has not been practicable to tow more than two Recorders at once). These attributes make possible a rapid coverage of a given area with minimum interruption by adverse weather conditions.

Although the Recorder can be very useful in a research vessel programme,

other instruments should be used to augment it. Metre nets may be used at selected stations, to get larger samples of undistorted specimens and to record vertical distributions, but the Hardy Recorder is an ideal instrument for filling in the coverage between stations.

With this kind of coverage concentrations of eggs and larvae can be delimited in a reasonable length of time and can be located again and re-surveyed at later dates. In our own programme, the drift of haddock eggs and larvae has been followed for several months through the technique of Hardy Recorder surveys. The same collections were adequate to provide important information on the distribution of key copepods and indicator species of diatoms.

Possibly because of the relatively high towing speed and the absence of bridles or other obstructions in front of the sampling aperture, the Recorder appears to catch more of the larger, active, larvae than are taken by conventional nets. The diurnal variation of numbers of larvae which is often noticed in the catches of slow moving nets (resulting presumably from daylight avoidance of the sampler) was not apparent in the Recorder collections of haddock and cod larvae.

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Galveston Biological Laboratory
U. S. Bureau of Commercial Fisheries

Survival of Stained, Tagged, and Unmarked Shrimp in the Presence of Predators

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Abstract

The survival rate of tagged, stain-marked, and unmarked shrimp held in tanks of sea water has been compared. Predaceous fish were introduced into the tanks and predation upon the three groups of shrimp compared. Unmarked shrimp and shrimp marked with biological stains survived at approximately the same rate with respect to each other with or without predators present; tagged shrimp incurred excessive mortality exclusive of predation and highly variable mortality with predators present.

DETERMINATION OF MORTALITY rates in populations of marine shrimp presents a challenging problem. Estimation of these important parameters using commercial fishery statistics has not yet proved feasible whereas their measurement by means of mark-recapture experiments promises an immediate solution. Successful application of the mark-recapture technique requires, in the case of any species, knowledge of the extent to which the experimental animals are affected by the type of mark employed. This is particularly significant in the case of shrimp since they are comparatively delicate organisms.

In the first large-scale effort to apply the mark-recapture method in studying the dynamics of shrimp populations, Lindner and Anderson (1956) made extensive use of tags to determine growth and migratory patterns in the white shrimp, *Penaeus setiferus*. These tags consisted of two celluloid (Petersen type) discs affixed, one on each side of the shrimp, by passing a nickel pin midlaterally through the first abdominal somite. Although this method has since been used by others, very few observations concerning the effect of tagging on the behavior and survival of individual shrimp have been reported. Lindner and Anderson (1956) and Iversen and Jones (1961) note that mortality due to tagging appears to be inversely related to size of shrimp tagged, their experiments having been characterized by proportionately fewer returns of small shrimp. From observations of captive pink shrimp, *Penaeus duorarum*, tagged with discs, the present authors conclude that attachment of such tags results in considerable loss of swimming efficiency.

Recognizing the major disadvantages of the tagging method, Menzel (1955) introduced and Dawson (1957) developed a method with fewer limitations, namely, marking with biological stains. The utility of the stain-marking method in shrimp migration studies has been demonstrated by Costello (1959) and Costello and Allen (1960). In anticipation of employing this technique in

Third Experiment

This experiment differed from the first in that one half as many shrimp (3 were used and that as predators a red grouper, *Epinephelus morio,* and a bl grouper, *Mycteroperca bonaci,* replaced the four snappers. Stomachs of the groupers at the experiment's termination contained, in one case, three parti digested shrimp and no tags, and in the other, two shrimp and one pair of t

Discussion:

Specifications and results of the three experiments are summarized in Tabl From these may be drawn the following inferences concerning relative surv (under natural conditions) of stained, tagged, and unmarked shrimp:

1. Whether predators be present or absent, tagged shrimp may be expected suffer higher mortality than either stained or unmarked shrimp. [Comparin with that of the unmarked (control) group, mortality due to tagging in 10-day period ranged from 20 per cent (first experiment, south tank) to per cent (third experiment, north tank).]

2. Tagged shrimp may be expected to be proportionately more vulnerable predation than stained shrimp.

3. If reasonable care is taken during marking operations, shrimp marked w biological stains may be expected to survive at essentially the same rate unmarked shrimp whether or not predators are present. [Shrimp marked w biological dyes, in fact, survived at a slightly better rate than unmarked shri perhaps due to some prophylactic effect of the stains.]

Due to the limited scope of these experiments, the results must be conside preliminary. They do indicate, however, that a more successful application the mark-recapture method in shrimp population studies can be achieved if experimental shrimp are marked with biological stains, rather than "mech cal" tags.

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THE 1960 PRESEASON ALBACORE SURVEY IN THE NORTHEASTERN PACIFIC OCEAN[1]

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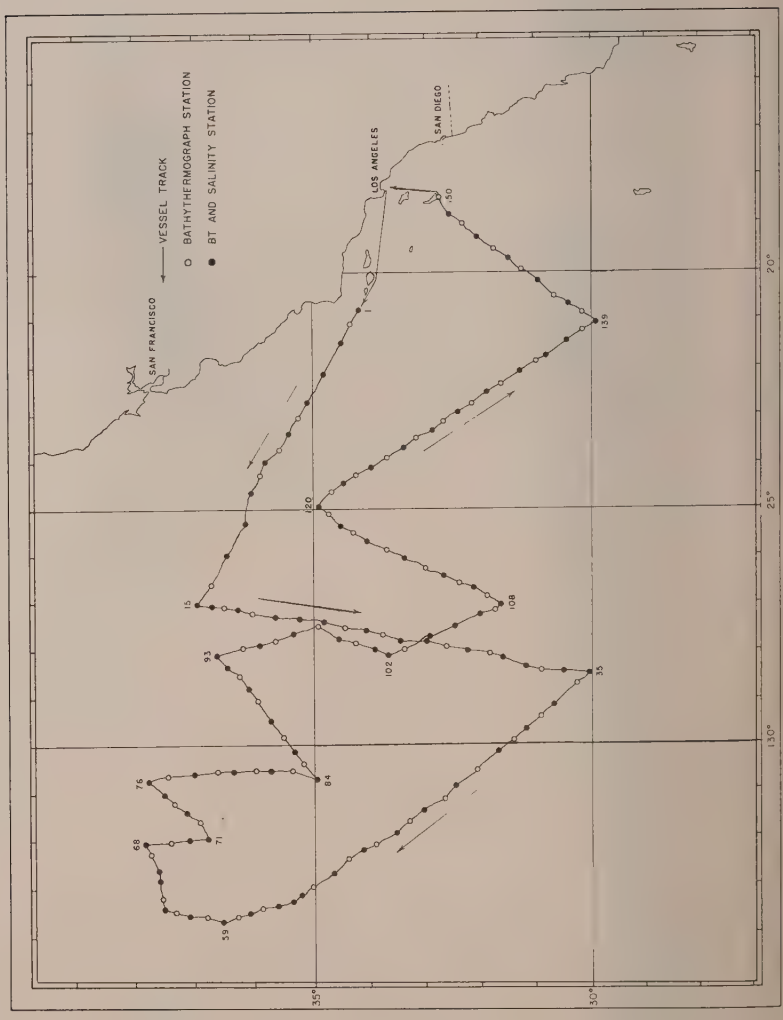
INTRODUCTION

The California Department of Fish and Game has conducted several xploratory fishing and oceanographic cruises to study albacore *(Thunus germo)* and their environment prior to the regular fishing season Craig and Graham, 1961; Graham and Craig, 1961). These surveys ave been conducted during the spring, to learn more about the movenents of these economically valuable tuna prior to and during the eginning of the annual fishing season. Although a great deal has been earned about their movements through a tag-and-recovery program Clemens, 1961; Otsu, 1960) and by studying catch records (Clemens, 955), their migration route into the American fishing grounds needs dditional investigation.

The location of early-season albacore concentrations is vitally imortant to commercial fishermen, for they must be prepared to catch large portion of the season's total within three months after the fish ppear in local waters. Because albacore are a popular sport fish and he season is short, recreational fishermen become frenzied by the appearance of the early migrants. Thus, locating and charting the progress f inbound schools enables scientists to study albacore and their enironment, and by relaying the information to sport and commercial shermen great savings of tedious and expensive scouting time are ealized.

A program of oceanographic observations for the 1960 survey was lanned and carried out, in co-operation with the U.S. Bureau of Comercial Fisheries, Biological Laboratory, San Diego, to determine relaionships between the physical environment and albacore movements uring their entry into the West Coast fishing grounds. A series of hese ecological data should enable us to make more refined predictions f albacore movements when coupled with advance knowledge of enironmental conditions. Toward this end, the present report embodies compilation and a limited analysis of the physical and biological nformation collected during the 1960 survey.

Submitted for publication August 1961.


VESSEL TRACK
BATHYTHERMOGRAPH STATION
BT AND SALINITY STATION
SAN FRANCISCO
LOS ANGELES
SAN DIEGO
120°
125°
130°
35°
30°
20°
1
15
39
68
71
76
84
93
102
108
120
139
150
35

CRUISE PLAN

For the second consecutive year the Department of Fish and Game vessel *N. B. Scofield* (Cruise 60S3) was used in an effort to intercept the incoming albacore schools by fishing along three predetermined lines between Cape Mendocino, California, and Punta Baja, Baja California. Should albacore be caught on one of these fishing lines, the cruise pattern was to be modified in an attempt to outline their latitudinal range while following them coastward (Figure 1).

The vessel proceeded from San Pedro toward the initial trolling line the evening of May 23 and returned to port 26 days later on June 18, 1960.

Fishing Method

Surface trolling gear was used to locate albacore schools. Artificial lures consisting of feathered japheads, and various plastic or bone jigs were attached to 6 or 7 lines of various lengths and trolled during daylight hours. Barbless hooks were used so that fish in good condition could be unhooked quickly for tagging. Trolling speed varied from 6 to 10 knots and averaged 6 to 7.

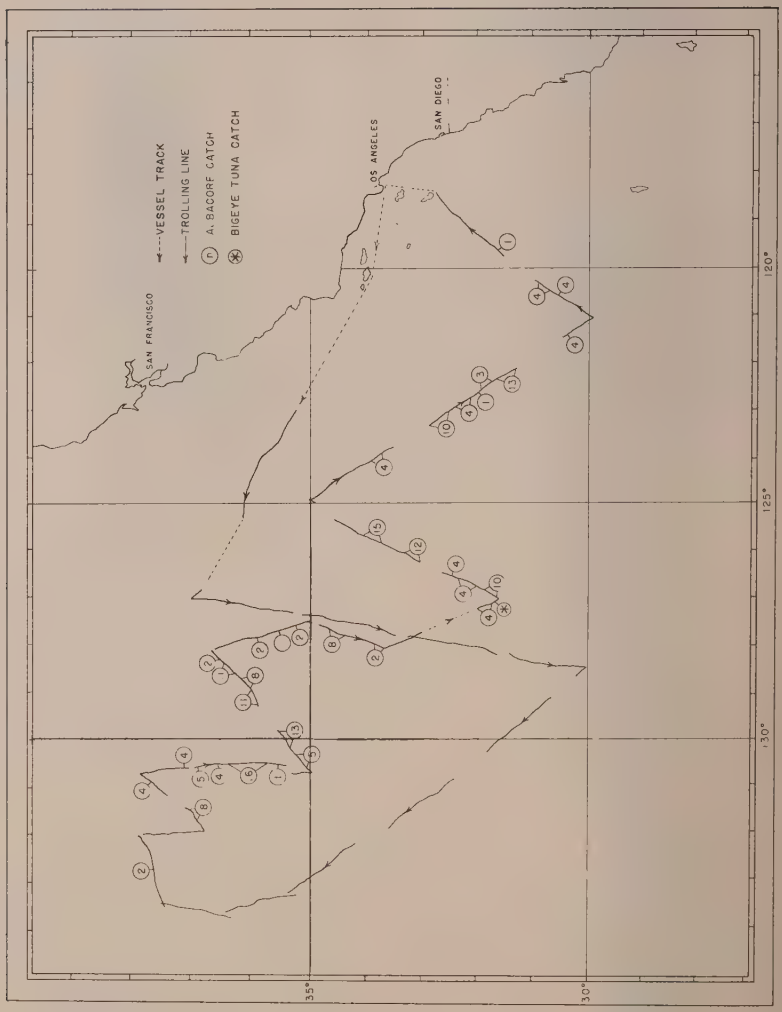
Plans to carry a small supply of live anchovies *(Engraulis mordax)* for bait fishing, in the event large concentrations of albacore were located, were changed when the tidal effects of a severe Chilean earthquake roiled Los Angeles Harbor and ruined baiting for a few days.

Oceanographic Observations

The survey plans placed primary emphasis on trolling for albacore, and secondarily, on gathering the most pertinent oceanographic data with the least interference to the primary purpose. Sea temperature and salinity were selected as the most useful physical observations under these restricted conditions.

A comprehensive record of sea temperature was obtained by means of the bathythermograph (BT) as well as bucket and recording thermometers. Bathythermograph lowerings to 450 feet were made at intervals approximately 20 miles apart. At each BT station an accurate reading of surface temperature was obtained with a bucket thermometer. The recording thermometer operated continuously during the survey.

Water samples for salinity determination were collected from Nansen bottle casts to 33 foot (10 meters) depths at intervals approximating 40 miles or at alternate BT stations. All oceanographic stations were occupied while the vessel moved slow ahead (1 to 3 knots) since stopping to drift meant securing all the fishing gear and losing precious scouting time. Movement of the vessel at these speeds resulted in obtaining the samples from a different depth than they would have been obtained if the cable had dropped perpendicular to the sea surface. This was compensated somewhat by considering the wire angle and varying the amount of cable metered off the winch. Most of the water samples thus collected were from depths closely approximating 10 meters. In some instances, however, the necessary compensation could not be made and the resulting samples were taken in depths estimated between 20 and 56 feet (6 and 17 meters).


VESSEL TRACK
TROLLING LINE
A. BACORF CATCH
BIGEYE TUNA CATCH
SAN FRANCISCO
LOS ANGELES
SAN DIEGO
35°
30°
120°
125°
130°

Miscellaneous Observations

Several incidental observations were made to further the study of environmental conditions. Night light stations were attended while the vessel drifted on sea anchor. A 1,500-watt lamp was supended over the water at dusk and observations or collections were made throughout the evening. Weather and sea conditions were noted in connection with the BT log. Significant physical and biological occurrences or changes were also noted.

CRUISE RESULTS

Fishing Data

Trolling took place during daylight hours from approximately 120 miles west-northwest of Point Arguello to the south side of San Clemente Island. Slightly over 3,000 miles were traveled during the 26 days; nearly 2,300 miles were fished with trolling lines (Figure 2).

The first albacore were caught on the twelfth day of the cruise about 500 miles west of San Francisco (lat. 37° 43′ N., long. 132° 45′ W.). From that point, catches ranged from 1 to 26 fish each day throughout the remainder of the survey (Table 1).

For the sake of uniformity, no intense fishing effort was expended in any one area. By maintaining a straight course, fishing effort was evenly distributed allowing estimates of relative abundance between various areas. Catches of the *N. B. Scofield* indicated albacore were in greatest concentration in three localities: the northwestern area south of lat. 37° N. in close proximity to long. 130° W.; in the central portion south of lat. 34° N. and west of long. 125° W.; and southeast of the central portion west of long. 120° W.

The only other species caught on the trolling lines was bigeye tuna (*Parathunnus sibi*). Early in the morning of June 12, near Fieberling Guyot (lat. 32° 23′ N., long. 127° 49′ W.), all six lines hooked-up at the same instant. Five of the six fish broke off carrying the tackle with them. The sixth was landed and proved to be a bigeye tuna weighing approximately 50 pounds.

To further substantiate their coastward migration route, albacore were tagged at numerous offshore localities. Recoveries of preseason tagged fish early in the regular fishing season would aid materially in establishing a pattern of movement to the coast. Of 153 fish landed, 74 were considered in suitable condition and were tagged and released. None, however, was subsequently recovered.

Fork-length measurements on 135 of the 153 fish arranged as a size frequency distribution, show 90 percent of the fish averaged 12 pounds each. This is the size group usually dominating the Pacific coast fishery (Clemens, 1961). The remaining 10 percent consisted of fish in three size groups, averaging 7, 18, and 25 pounds each; these contribute to the commercial fishery in lesser quantities (Table 2).

Oceanographic Observations

In addition to sea-surface temperature measurements, 450-foot bathythermograph casts were made at 150 stations during the cruise (Figure 1). Water samples for salinity determination were collected at 85 positions. Generally the samples were obtained at alternate BT stations though occasional exceptions were necessary to complete the data (Figure 1).

TABLE 1

Albacore Catch Localities for the N. B. SCOFIELD Scouting Cruise (60S3)
May 23 to June 18, 1960

Date	Position		Number tagged	Number saved	Number lost	Total catch	Surface Temperature (Degrees F.)
	N. lat.	W. long.					
6/4/60	37°43′	132°45′	--	2	--	2	61.1
6/5/60	37°02′	131°39′	--	2	--	2	62.1
	37°04′	131°37′	--	2	--	2	61.9
	37°06′	131°33′	1	2	1	4	61.7
6/6/60	37°46′	130°52′	1	2	1	4	59.5
	37°10′	130°38′	1	1	--	2	61.9
	37°07′	130°38′	2	--	--	2	61.9
6/7/60	36°57′	130°37′	1	2	2	5	62.1
	36°36′	130°35′	2	--	2	4	62.1
	36°24′	130°36′	--	--	1	1	60.6
	36°12′	130°36′	1	1	--	2	62.6
	36°07′	130°36′	--	--	1	1	62.4
	36°03′	130°36′	--	--	1	1	62.2
	36°01′	130°36′	1	1	--	2	62.4
	35°56′	130°36′	--	2	3	5	62.4
	35°49′	130°36′	2	2	--	4	62.8
	35°33′	130°36′	--	1	--	1	62.2
6/8/60	35°05′	130°35′	1	--	--	1	62.4
	35°07′	130°31′	1	--	1	2	62.4
	35°12′	130°23′	1	--	1	2	62.6
	35°22′	130°06′	--	2	--	2	62.4
	35°27′	129°57′	1	1	--	2	62.6
	35°30′	129°52′	6	2	1	9	62.1
6/9/60	35°52′	129°17′	2	2	--	4	61.0
	35°53′	129°15′	2	--	--	2	61.0
	35°56′	129°11′	--	1	--	1	61.0
	35°57′	129°08′	1	2	--	3	61.2
	36°03′	129°00′	--	1	--	1	61.0
	36°03′	128°57′	1	1	1	3	61.0
	36°07′	128°52′	1	--	--	1	61.0
	36°14′	128°42′	1	2	1	4	61.2
	36°19′	128°34′	--	4	--	4	60.8
	36°23′	128°30′	3	--	2	5	60.6
	36°25′	128°28′	1	--	1	2	60.6
	36°32′	128°19′	--	1	1	2	59.9
6/10/60	35°53′	127°53′	--	1	1	2	60.4
	35°29′	127°45′	--	1	--	1	60.8
	35°14′	127°39′	1	--	--	1	60.8
6/11/60	34°37′	127°43′	1	2	--	3	60.6
	34°31′	127°46′	--	1	--	1	61.3
	34°26′	127°47′	2	--	1	3	61.3
	34°25′	127°49′	--	--	1	1	61.5
	33°52′	128°02′	1	--	--	1	62.3
	33°43′	128°05′	1	--	--	1	62.6
6/12/60*	32°01′	127°15′	--	--	1	1	64.1
	32°00′	127°14′	--	1	1	2	64.2
	31°53′	127°11′	--	1	--	1	64.0
	31°38′	127°01′	2	--	2	4	63.5
	31°40′	127°00′	1	--	1	2	63.5

* One bigeye tuna caught at lat. 31°43′N., long. 127°06′W., surface temperature 64.2°F.

TABLE 1—Continued

Albacore Catch Localities for the N. B. SCOFIELD Scouting Cruise (60S3)
May 23 to June 18, 1960

Date	Position		Number tagged	Number saved	Number lost	Total catch	Surface Temperature (Degrees F.)
	N. lat.	W. long.					
12/60*_____	31°46′	126°56′	1	--	--	1	63.5
	31°48′	126°55′	--	2	1	3	63.5
	32°08′	126°45′	--	1	--	1	63.5
	32°12′	126°41′	1	--	--	1	63.3
	32°17′	126°39′	1	--	--	1	63.3
	32°19′	126°38′	--	--	1	1	63.3
	32°27′	126°33′	2	--	2	4	63.7
6/13/60_____	33°02′	126°14′	--	1	--	1	62.8
	33°04′	126°13′	1	--	1	2	62.8
	33°16′	126°06′	1	--	--	1	62.8
	33°18′	126°05′	4	2	2	8	62.8
	33°47′	125°50′	1	1	1	3	61.0
	33°52′	125°47′	2	--	--	2	61.0
	33°57′	125°44′	2	2	3	7	61.0
	33°58′	125°43′	--	--	1	1	61.0
	34°02′	125°41′	1	1	--	2	61.2
6/14/60_____	33°54′	124°06′	--	2	1	3	60.1
	33°47′	124°00′	1	--	--	1	60.3
6/15/60_____	32°51′	123°20′	--	1	--	1	60.4
	32°49′	123°18′	--	3	1	4	60.6
	32°46′	123°16′	--	2	--	2	60.6
	32°38′	123°09′	3	--	--	3	61.0
	32°21′	122°56′	--	1	1	2	61.3
	32°17′	122°53′	1	--	--	1	61.5
	32°14′	122°15′	--	--	1	1	61.5
	31°59′	122°39′	--	1	--	1	61.7
	31°55′	122°35′	1	1	--	2	61.7
	31°45′	122°29′	--	1	--	1	61.7
	31°37′	122°22′	--	--	1	1	61.5
	31°34′	122°20′	1	2	2	5	61.5
	31°30′	122°17′	--	1	--	1	61.5
	31°27′	122°15′	--	1	--	1	61.5
	31°25′	122°12′	2	1	--	3	61.7
	31°20′	122°10′	1	1	--	2	61.7
6/16/60_____	30°21′	121°24′	--	3	1	4	61.5
	30°28′	120°36′	1	1	2	4	62.8
	30°40′	120°27′	1	--	--	1	62.6
	30°44′	120°24′	--	--	1	1	62.4
	30°48′	120°20′	2	--	--	2	62.6
6/17/60_____	31°34′	119°42′	--	1	--	1	60.4
TOTALS ..	------	-------	74	79	52	205	----

* One bigeye tuna caught at lat. 31°43′N., long. 127°06′W., surface temperature 64.2°F.

TABLE 2

Length Frequency Distribution of 135 Albacore Caught During the Albacore Survey, May 23 to June 18, 1960

Length (cm)	Frequency	Percent	Length (cm)	Frequency	Percent
51	2	1.5	66	9	6.7
56	1	0.7	67	4	3.0
60	1	0.7	75	1	0.7
61	5	3.7	76	2	1.5
62	16	11.9	77	5	3.7
63	29	21.5	78	1	0.7
64	38	28.1	81	1	0.7
65	19	14.1	82	1	0.7

Surface water temperature ranged from 51.3 degrees F. around t northern Channel Islands to 65.3 degrees F. 400 to 500 miles west Point Arguello. Salinities varied from 32.90 parts per thousand stations within 200 miles west of Monterey, to 33.95 parts per thousa in the extreme southwestern area. Albacore catches were restricted temperatures between 59.5 and 64.2 degrees F. and salinities betwe 32.95 and 33.53 parts per thousand. Superimposing the catches up isograms of sea temperature and salinity illustrates their relationsh to the distribution of these physical properties (Figures 3 and 4).

Vertical temperature profiles were prepared from selected B slides to relate areas of good fishing with subsurface temperatu changes or with the thermocline depth. Cursory examination failed show any obvious relationship hence further analysis was discontinue Temperatures were tabulated at standard depths for each BT ca (Table 3).

Miscellaneous Details

Nine night-light stations were occupied while the vessel drifted a sea anchor. Small Pacific sauries (*Cololabis saira*) showed up varying numbers at all but one station which was located in the nort western area at lat. 35° 23′ N., long. 130° 36′ W. Other organisn observed at fewer stations were jack mackerel (*Trachurus symmet cus*), lantern fish (Family Myctophidae), shark, squid and tunicat (Table 4).

Stomachs of most of the 79 fish unfit for tagging, were examine qualitatively in the field to determine the nature and extent of feedin Most were empty or contained only a small amount of nearly digest material. Among the more common recognizable organisms were Paci saury, jack mackerel and cephalopods. Several stomachs contain unfamiliar organisms in reasonably good condition. These were froz and returned to the laboratory for identification (Table 5).

Two parasitic helminths occurred commonly in the albacore sto achs; one was a nematode and the other a trematode. These have n been positively identified, but their striking resemblance to illustr tions of the nematode *Contracaecum legendrei* and the tremato *Hirudinella fusca* from albacore caught in the eastern Atlantic Oce (Dollfus, 1940) suggests a generic relationship between these parasit in the two oceans.

Daytime observations were typical of those encountered in the same area on previous cruises. One small whale and two sea lions were the only mammals observed. Albatross were present in small numbers most of the time. Storm petrels, though less prevalent, were frequently observed. Behavior of the birds appeared no different in areas where fish were caught and at no time did feeding birds indicate the presence of fish. Two vast areas of *Velella lata* were noted: one, near San Miguel Island, extended for approximately 60 miles, the other for about 30 miles near the location of the first albacore catch. Numerous glass net-floats were seen, particularly in the north-central portion of the survey area. Most of these were heavily encrusted with stalked barnacles indicating a long period of drifting in the sea.

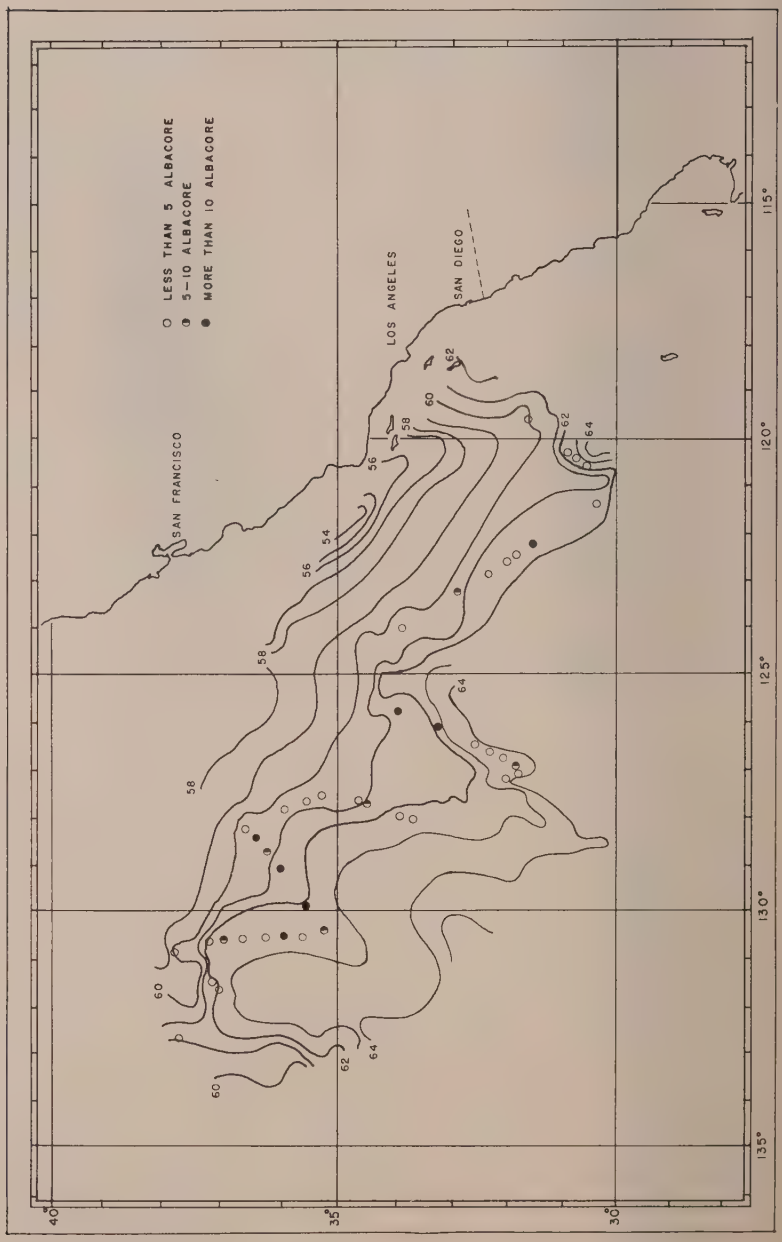
While running the last survey line, the sea itself proved interesting to observe. Characteristic "tide rips," typical of an area where water masses converge (Sverdrup, *et al.*, 1942), were visible in all directions. The recording thermometer sometimes fluctuated plus and minus one degree C. in less than five minutes. The water remained clear, but the color in some of the "fingers" was greenish and contained floating kelp, while in others oceanic blue color prevailed without kelp.

DISCUSSION

Japanese workers have suggested that albacore may be identified with a distinct current system (Nakamura, 1954; Suda, 1956). With this in mind the *N. B. Scofield* cruise data were examined for evidence of such an alliance in the California Current system during the spring albacore migration.

It is possible to estimate water mass transitions taking place during the cruise by analyzing the temperature-salinity structure (Miller, 1950), (Figure 5). In the area of Point Conception, temperatures were much cooler than any subsequently encountered, yet salinities were in the upper part of the range (Stations 1, 3 and 4). Such a temperature-salinity distribution is undoubtedly the result of upwelling along the adjacent coastline. Northwest of Point Conception and farther offshore, the stations shown between 5 and 18 (Figure 5) were characterized by a marked decline in salinity values, but only a slight increase in temperature. This combination is indicative of water transported by the California Current and presumably represents passage of the *N. B. Scofield* through the eastern boundary of this system. The grouping of values between 33.00 and 33.40 parts per thousand salinity and 60 to 63 degrees F. temperature constitutes data collected in the expanse of the California Current itself. Values in excess of these probably represent the transition from the California Current to the warmer more saline water of the central northeastern Pacific Ocean.

Investigators have often used the horizontal temperature-salinity profile to relate a biological entity to different water masses (Bary, 1959). With the albacore this approach provides an interesting distribution. Most of the albacore were taken in a restricted range of temperatures and salinities (Figure 5). Of the catch, 87 percent was landed in water of 60.5 to 63.0 degrees F. and in salinities from 33.05 to 33.30 parts per thousand. Averages for June (1949 through 1959)


LESS THAN 5 ALBACORE
5–10 ALBACORE
MORE THAN 10 ALBACORE
SAN FRANCISCO
LOS ANGELES
SAN DIEGO
40°
35°
30°
115°
120°
125°
130°
135°

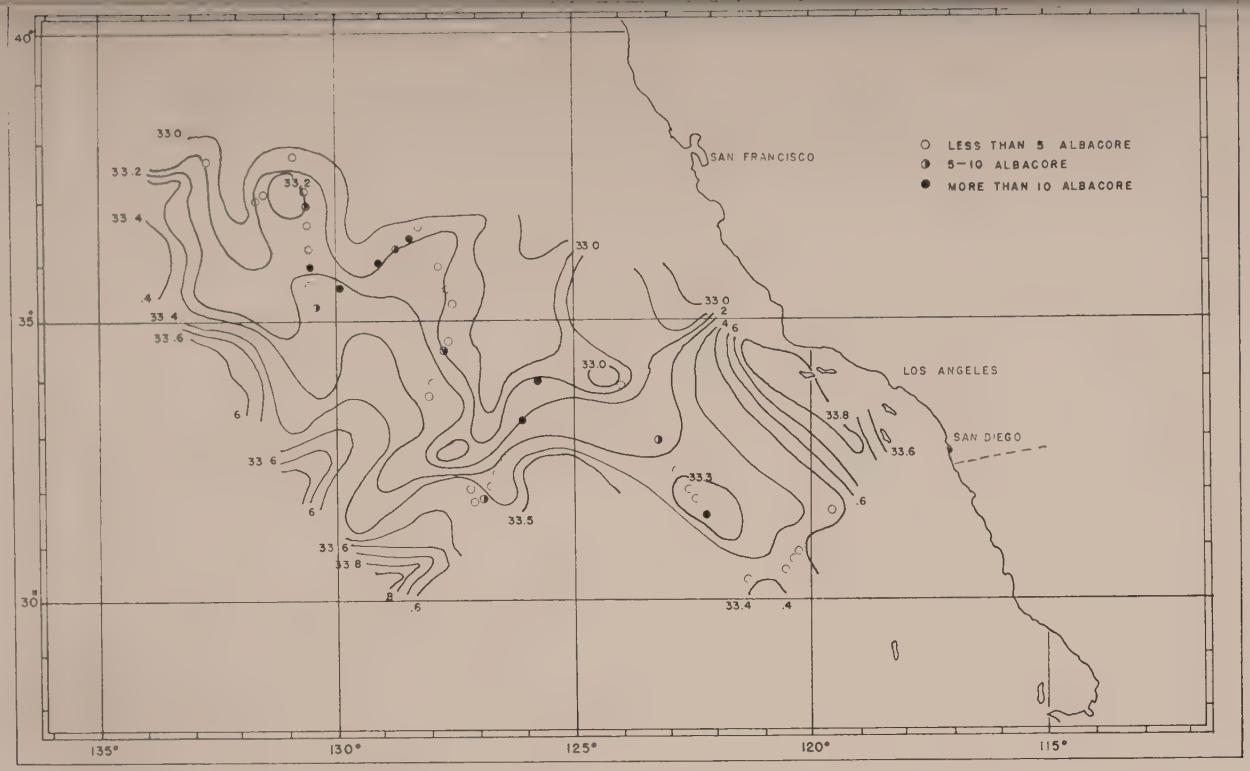


FIGURE 4. Ten-meter salinity contours by 0.10 parts per thousand (0/00) intervals showing relationship of albacore catches made during the 1960 survey.

TABLE 3

Summary of Observations at Bathythermograph Stations Occupied During the Albacore Survey, May 23 to June 18, 1960

Serial No.	Date	Time GMT	Location N. lat.	Location W. long.	Depth (fm)	Salinity ‰ (10M)	Barometer (mb)*	TEMPERATURE (°F.) Air Wet	Air Dry	Water Bucket (surface)	Bathythermograph (depth in feet) 0	30	50	100	150	200	250	300	330	400	490	500	600	655	700
1a	V-24	2318	34-10	120-47	430	33.87	1016	58.0	59.0	55.8	55.2	52.9	52.5	51.3	50.4	48.9	48.0	47.5	47.1						
1b	V-24	2325	34-10	120-47	430	———	1016	58.0	59.0	55.8	55.8	52.7	52.5	51.1	49.3	48.6	48.0	47.5	47.3	47.1	47.1	46.9	46.9		
2	V-25	0131	34-19	121-07	860	———	1017	57.0	58.0	55.4	54.9	51.8	51.6	50.9	49.6	48.6	48.0	47.5	47.1						
3	V-25	0353	34-29	121-30	1000	33.79	1017	55.5	57.0	54.1	54.1	51.6	51.3	51.1	50.9	50.5	49.8	48.4	47.5						
4	V-25	0803	34-47	122-10	2100	33.47	1018	55.0	56.0	54.0	53.6	52.5	52.5	51.6	51.4	50.4	50.2	49.5	48.9						
5	V-25	1148	35-05	122-45	———	33.15	1018	55.0	57.0	55.8	55.9	55.9	55.6	55.2	54.5	53.4	52.9	52.0							
6	V-25	1400	35-17	123-06	2100	———	1019	58.0	60.0	56.8	56.7	56.1	55.4	55.2	55.2	54.3	54.0	53.8	52.3	49.8					
7	V-25	1601	35-26	123-26	1700	33.04	1020	60.0	64.0	57.7	57.2	56.5	56.1	55.2	55.0	53.6	52.3	51.4	50.5	48.2					
8	V-25	1802	35-35	123-46	2100	———	1020	60.0	63.5	57.2	56.5	54.9	54.1	52.3	51.8	51.1	50.9	50.2							
9	V-25	2001	35-49	124-01	2150	33.12	1021	61.0	64.0	58.5	57.9	57.0	56.8	56.1	54.9	53.6	52.0	50.5							
10	V-25	2201	35-56	124-19	2125	———	1022	60.0	63.0	57.0	56.7	55.6	55.6	54.3	52.5	52.0	50.5	49.6							
11	V-26	0028	36-05	124-43	2250	33.16	1021	61.0	63.5	58.6	58.3	57.9	57.9	57.6	57.4	55.0	52.7	50.7							
12	V-26	0414	36-12	125-20	2420	32.91	1022	59.0	60.5	57.7	57.7	57.7	57.4	57.0	56.8	56.7	54.3	53.6	53.2						
13	V-26	0803	36-29	125-58	2420	32.90	1022	58.5	59.0	57.7	57.9	57.9	57.2	56.1	55.9	55.2	54.3	54.1	54.3						
14	V-26	1153	36-48	126-37	2275	———	1020	58.0	59.0	57.7	58.8	58.8	58.8	58.3	57.9	56.3	55.9	55.2	54.7						
15	V-26	1430	37-00	127-00	———	32.99	1020	59.0	60.0	57.9	57.9	57.9	57.9	57.6	57.4	56.5	54.5	54.0	53.1						
16	V-26	1602	36-47	127-03	2450	33.09	1022	60.0	62.0	58.5	58.6	58.6	58.6	58.3	58.3	56.8	55.8	54.5	54.3						
17	V-26	1758	36-33	127-06	2450	———	1022	61.0	62.5	58.6	59.0	59.0	58.8	58.6	58.1	56.5	54.5	54.1	54.1						
18	V-26	1956	36-19	127-09	2525	32.99	1022	62.0	64.0	58.5	59.7	59.5	59.4	59.2	56.1	55.8	55.4	53.8	53.1						
19	V-26	2200	36-04	127-12	2500	———	1025	61.5	63.0	59.7	59.7	59.4	59.2	58.1	57.9	56.8	55.4								
20	V-27	0050	35-41	127-17	2500	33.04	1025	60.0	61.0	59.7	59.7	59.0	58.8	58.5	58.5	57.0	56.3	55.6							
21	V-27	0350	35-16	127-21	2480	33.04	1026	59.0	60.0	60.1	60.1	59.9	59.5	58.6	58.5	58.3	55.8	54.7							
22	V-27	1602	34-51	127-28	2575	33.02	1027	56.0	59.0	60.1	60.1	59.9	59.9	59.4	57.9	56.7	55.8								

23	V-27	1000	34-27	127-33	2580	-------	1027	55.0	59.0	61.0	61.2	61.2	61.0	60.1	59.2	56.8	55.9	55.2											
24	V-27	2201	34-06	127-37	--	33.14	1027	58.0	62.0	61.3	61.5	61.5	61.3	60.4	60.1	57.9	55.8	54.9											
25	V-28	0053	33-46	127-42	2500	-------	1025	57.0	62.0	61.5	61.9	61.9	61.9	61.0	60.8	57.6	55.6	54.1	53.4										
26	V-28	0025	33-29	127-46	2350	33.26	1021	56.5	60.0	61.7	61.9	61.9	61.9	60.8	60.6	56.5	54.7	52.0	52.7	50.4									
27	V-28	1851	33-01	127-51	2430	33.23	1022	56.0	59.0	61.7	61.9	61.9	61.9	61.5	61.0	60.1	59.7	59.7	59.5	59.7									
28	V-28	1023	32-58	127-56	2300	-------	1022	57.0	59.0	61.9	62.1	62.1	62.1	61.9	61.3	59.9	59.9	59.9											
29	V-28	2230	32-11	128-02	2225	33.40	1022	58.0	61.0	62.8	62.8	62.8	62.6	62.4	61.9	61.7	59.9	60.8											
30	V-28	2332	31-50	128-07	2280	-------	1021	57.5	62.0	63.1	63.1	63.1	63.1	63.1	63.0	62.8	60.8	59.2											
31a	V-29	0317	31-37	128-12	2210	33.51	1021	57.0	60.0	62.8	63.3	63.3	63.3	63.3	62.8	61.9	60.8	59.7	58.1	54.5									
31b	V-29	0322	31-37	128-12	2210	-------	1021	57.0	60.0	62.8	63.0	63.0	63.0	62.2	61.7	60.6	59.0	57.0	55.6	51.8	48.6	48.4	47.3	46.9	46.6				
32	V-29	1601	31-11	128-21	2280	33.50	1022	59.0	63.0	63.1	63.3	63.5	63.3	62.8	62.8	61.5	60.8												
33	V-29	1830	30-53	128-26	2350	-------	1023	61.0	64.0	63.5	63.7	63.7	64.4	64.2	62.2	62.6	61.5	60.8											
34	V-29	2132	30-31	128-29	2400	33.95	1023	61.5	65.0	64.6	65.1	65.1	65.1	64.8	64.8	63.7	62.4	63.1											
35	V-30	0132	30-00	128-30	2300	33.55	1022	61.0	63.0	64.2	64.0	64.0	64.0	65.1	64.9	64.9	64.4	63.9	64.4										
36	V-30	0503	30-15	128-44	2560	-------	1023	62.5	65.0	64.8	64.9	64.9	64.9	64.4	64.1	62.6	62.8	63.0											
37	V-30	1402	30-40	129-11	2400	33.91	1023	61.5	63.0	64.6	64.9	64.9	64.9	64.9	64.0	63.9	63.9	65.5	65.5										
38	V-30	1701	30-56	129-26	2400	-------	1022	62.0	65.0	64.4	64.2	64.2	64.2	64.8	63.7	63.1	63.9	63.7	63.1	63.0									
39	V-30	2001	31-11	129-41	2400	33.68	1022	61.5	66.5	64.8	64.9	64.8	64.8	64.2	64.0	62.2	61.0	61.0	61.0	61.7									
40	V-30	2302	31-27	129-55	2425	-------	1025	61.5	65.5	64.2	64.8	64.8	64.4	64.2	63.9	62.2	61.2	60.8	60.6	60.6									
41	V-31	0201	31-11	130-00	2400	33.39	1023	61.5	65.0	64.1	64.8	64.6	64.0	62.8	62.4	61.0	61.1	60.4	60.1										
42	V-31	0759	32-07	130-33	2380	-------	1025	61.5	64.0	64.8	64.8	64.8	64.8	63.5	63.0	61.5	60.3	60.3	60.4										
43	V-31	1431	32-31	130-56	2400	33.70	1026	61.5	64.0	65.7	65.8	65.8	65.8	64.6	61.2	60.8	60.8	60.8	61.3										
44	V-31	1732	32-46	131-09	2200	-------	1027	62.0	64.0	65.5	65.5	65.5	64.6	63.9	63.5	61.7	61.3	62.4	60.4										
45	V-31	2101	33-01	131-24	2350	33.41	1027	63.0	67.0	64.0	64.0	64.0	63.9	63.5	62.1	59.9	59.7	61.0	59.2										
46	V-1	0002	33-19	131-39	2510	-------	1027	62.0	64.5	63.7	63.7	63.7	63.1	62.6	60.8	60.8	60.8	60.8	61.9										
47	V-1	0302	33-34	131-54	2625	33.66	1026	61.0	61.5	63.7	63.9	63.9	63.9	62.8	61.1	61.0	60.8	60.6	60.6										
48	V-1	0908	33-55	132-08	2775	-------	1025	62.0	65.0	63.7	63.9	63.9	63.9	62.4	62.2	61.7	61.1	61.0	61.0										
49	V-1	1353	34-09	132-15	2700	33.58	1025	60.5	61.5	63.3	63.3	63.3	63.3	62.4	62.1	61.0	61.0	61.1	61.3	60.8									
50	V-1	1701	34-26	132-28	2830	-------	1026	63.0	65.0	64.6	64.2	64.2	64.2	62.8	62.8	63.3	62.4	62.6	62.2										
51	V-1	2009	34-43	132-41	2200	-------	1026	62.0	65.0	62.4	63.3	63.1	63.0	61.9	61.3	60.6	60.3	60.6	60.1										
52	V-1	2304	35-01	133-01	2650	-------	1025	62.0	64.0	60.8	61.7	61.7	61.3	59.7	59.7	60.1	59.9	60.1	59.4										
53	V-2	0152	35-14	133-13	2700	33.33	1024	62.0	64.0	62.6	63.0	63.0	62.2	59.7	59.7	61.7	58.6	56.5	55.6	57.0									
54a	V-2	0407	35-21	133-20	2660	33.19	1024	61.0	62.0	61.7	61.5	61.5	61.5	59.7	58.8	57.0	57.2	59.2	58.6	55.4									
54b	V-2	0412	35-21	133-20	2660	33.19	1024	61.0	62.0	61.7	61.0	60.8	59.9	59.9	56.3	55.6	57.9	57.2	57.7	55.4	51.6	50.7	47.7	46.8	46.4				
55	V-2	1804	35-36	133-26	2450	33.30	1022	60.5	62.0	59.4	59.0	59.2	59.0	57.9	57.0	57.2	56.7	56.8	56.7	55.9									
56	V-2	2055	35-53	133-30	2680	-------	1022	63.0	64.5	60.1	59.9	59.7	59.7	57.6	57.0	56.5	55.4	54.7	54.7	55.2									
57	V-3	0003	36-06	133-35	2780	33.40	1021	62.0	63.5	60.3	60.1	60.1	60.1	58.5	57.7	57.4	56.8	56.1	55.9	55.4									
58	V-3	0301	36-20	133-40	2750	-------	1021	61.0	63.0	60.4	60.3	60.3	59.9	59.9	57.9	57.2	56.8	56.8	57.2										
59	V-3	1701	36-35	133-47	2725	33.39	1020	59.0	61.0	59.5	59.7	59.7	59.7	58.5	58.1	57.7	57.6	56.5	56.5										
60	V-3	2000	36-52	133-43	2600	-------	1021	60.0	62.0	59.7	59.7	59.7	59.7	57.6	56.5	56.1	54.7	53.8	54.3	52.9									
61	V-3	2305	37-08	133-58	2770	33.30	1020	64.0	64.0	60.4	60.8	60.8	60.6	59.2	56.8	55.9	54.9	54.5	53.6										
62	V-4	0146	37-23	133-41	2675	-------	1020	59.0	61.0	60.3	60.4	60.4	60.4	58.8	58.1	55.8	54.7	54.0	54.3										
63a	V-4	0345	37-33	133-31	2650	33.31	1020	58.5	59.5	60.6	60.8	60.4	60.1	58.5	57.6	56.7	55.9	54.9	54.7	53.6									

TABLE 3—Continued

Summary of Observations at Bathythermograph Stations Occupied during the Albacore Survey, May 23 to June 18, 1960

Serial No.	Date	Time GMT	Location		Depth (fm)	Salinity ‰ (10M)	Barometer (mb)*	TEMPERATURE (°F.)																	
			N. lat.	W. long.				Air		Water															
										Bucket (surface)	Bathythermograph (depth in feet)														
								Wet	Dry		0	30	50	100	150	200	250	300	330	400	490	500	600	655	700
63b	VI-4	0353	37-33	133-31	2650	33.31	1020	58.5	59.5	60.6	60.4	59.0	57.9	57.6	56.1	54.9	54.3	53.8	52.9	52.0	49.8	49.6	46.2	47.8	47.5
64	VI-4	1705	37-34	133-16	2650	-------	1018	59.5	61.5	60.4	60.4	60.6	60.6	60.1	59.2	58.1	57.6	54.7	54.3						
65	VI-4	2002	37-40	132-55	2700	33.12	1018	60.0	62.5	60.8	61.2	61.0	60.8	59.0	58.5	58.1	57.7	55.9	55.6						
66	VI-4	2153	37-43	132-43	2720	33.08	1017	60.5	62.5	61.2	61.2	61.2	61.0	59.0	58.6	57.9	56.3	56.5	56.1	53.4					
67	VI-5	0101	37-50	132-21	2725	-------	1017	61.0	63.0	60.4	60.4	60.4	60.4	60.1	58.8	58.3	57.7	57.0	57.0	52.9					
68a	VI-5	0404	37-55	132-06	2550	33.13	1016	59.5	61.0	60.6	60.8	60.8	60.8	60.1	58.1	57.6	57.2	56.8	56.3	55.9					
68b	VI-5	0408	37-55	132-06	2550	33.13	1016	59.5	61.0	60.6	60.6	60.1	59.9	58.1	57.2	56.7	56.5	55.6	55.4	54.7	50.9	50.4	48.6	47.7	47.5
69	VI-5	1705	37-29	132-05	2725	-------	1014	61.0	63.0	59.9	60.3	60.3	60.3	59.5	57.9	56.7	54.9	55.6	55.2						
70	VI-5	2002	37-08	132-02	2450	33.17	1017	61.0	64.0	61.9	62.2	62.2	62.2	62.1	59.7	58.1	56.5	56.5	53.6						
71	VI-5	2302	36-48	131-59	2680	33.01	1014	63.5	67.0	63.0	63.0	61.7	61.7	60.1	59.4	58.1	56.3	53.2	51.8						
72	VI-6	0232	37-02	131-40	2575	-------	1013	61.0	64.0	61.9	62.2	61.9	61.7	61.2	59.2	57.7	55.6	54.1	52.7	50.0					
73	VI-6	0642	37-13	131-26	2500	33.24	1014	59.9	62.0	62.2	62.1	62.1	62.1	62.1	60.1	57.2	56.8	56.3	54.7	52.0					
74	VI-6	1304	37-25	131-15	2480	-------	1015	58.0	61.0	60.1	60.1	60.1	60.1	59.9	57.9	57.0	55.6	55.2	55.0	54.7					
75	VI-6	1657	37-37	131-03	2560	33.21	1017	59.0	62.0	60.4	60.3	60.3	60.3	59.7	57.9	57.2	56.1	56.1	55.4	54.3					
76	VI-6	2133	37-52	130-45	------	33.04	1019	58.5	61.0	59.0	58.8	58.8	58.8	58.5	57.4	56.8	55.8	55.2	54.9	54.0					
77	VI-7	0032	37-31	130-42	2100	-------	1019	57.0	59.0	59.4	59.7	59.7	59.7	57.0	56.5	55.2	54.3	54.0	53.4						
78a	VI-7	0412	37-05	130-38	------	33.19	1020	57.0	59.0	61.9	62.1	62.2	62.2	62.1	59.9	58.3	57.2	57.6	56.5	52.5					
78b	VI-7	0416	37-05	130-38	------	33.19	1020	57.0	59.0	61.9	61.9	61.9	61.9	59.9	58.1	56.5	57.4	55.6	53.4	50.5	50.0	49.6	48.0	47.1	
79	VI-7	1702	36-41	130-36	2650	-------	1022	55.0	59.0	62.2	62.1	62.1	62.1	62.1	58.1	57.7	57.4	57.2	56.1						
80	VI-7	1933	36-24	130-36	2700	33.17	1023	57.0	62.0	62.6	63.0	63.0	63.0	61.2	58.6	58.1	58.1	57.7	58.3						
81	VI-7	2231	36-03	130-36	2575	-------	1023	58.0	62.5	62.6	62.6	62.6	62.6	61.7	58.6	57.4	57.2	56.7	56.7						
82	VI-8	0102	35-46	130-36	2690	33.25	1022	57.0	61.0	63.0	62.4	62.4	62.4	60.8	58.1	57.2	56.8	54.7	56.3						
83a	VI-8	0408	35-23	130-36	2650	-------	1022	56.0	59.0	62.6	62.6	62.6	62.6	60.3	58.5	57.9	57.0	56.7	56.1	55.6					
83b	VI-8	0412	35-23	130-36	2650	-------	1022	56.0	59.0	62.6	62.4	62.4	62.4	58.8	57.9	57.0	56.7	55.6	55.2	53.6	49.3	49.1	48.2	47.1	46.9

85	VI-8	2115	35-10	130-26	2575	---- ---	1022	58.0	63.0	62.6	62.8	62.8	62.8	61.0	58.6	57.6	57.0	55.2	55.0						
86	VI-9	0032	35-20	130-09	2560	33.25	1022	57.0	61.0	62.4	62.4	62.4	62.4	61.5	61.7	60.6	60.1	57.7	56.7	56.3					
87	VI-9	0416	35-31	129-50	2560	---- ---	1022	56.0	58.0	61.9	62.1	62.1	62.1	60.8	59.7	59.2	58.5	58.6	57.9	56.8					
88	VI-9	1003	35-44	129-30	2580	33.09	1021	55.5	59.5	61.3	61.5	61.5	61.5	61.3	59.9	58.5	57.2	57.2	56.1						
89	VI-9	1547	35-58	129-06	2540	-------	1021	57.1	58.9	61.2	61.5	61.5	61.5	61.5	59.7	57.9	56.8	56.1	55.8	54.1					
90	VI-9	1901	36-08	128-51	2550	33.12	1021	59.0	62.0	60.8	61.0	61.0	61.0	61.0	58.8	57.6	56.3	55.4	55.2	52.7					
91	VI-9	2201	36-18	128-35	2590	---- ---	1021	59.0	61.0	60.8	61.0	61.0	61.0	61.0	60.8	59.7	58.3	57.9	58.3						
92	VI-10	0103	36-29	128-22	2540	33.08	1020	58.5	61.0	60.8	60.8	60.8	60.8	60.6	59.9	58.3	58.1	56.7	56.3	56.8					
93	VI-10	0408	36-40	128-08	2520	33.10	1020	56.5	59.0	60.1	60 1	60.1	60.1	60.1	59.9	57.9	56.8	56.5	56.5	53.6					
94	VI-10	1623	36-14	127-59	2450	---- ---	1023	57.0	61 0	59.5	59.5	59.5	59.5	59.5	59.5	58.3	56.3	56.1	55.8						
95	VI-10	1902	35-55	127-54	2100	33.12	1023	57.0	61.0	60.8	60.8	60.8	60.8	60.8	60.6	59.0	56.8	55.8	55.2						
96	VI-10	2138	35-37	127-17	2500	---- ---	1023	58.0	61.0	60.8	60.6	60.6	60.6	60.6	58.8	58.1	56.1	55.4	55.4						
97	VI-11	0002	35-20	127-41	2550	33.08	1023	58.0	61.0	60.8	60.4	60.1	60.4	60.4	58.3	57.4	56.1	55.2	54.9						
98a	VI-11	0315	34-57	127-32	2500	---- ---	1023	57.0	59.0	60.4	60.3	60.3	60.3	60.3	59.0	57.0	56.0	55.6	55.4	53.8					
98b	VI-11	0322	34-57	127-32	2500	---- ---	1023	57.0	59.0	60.4	60.4	60.4	60.4	59.4	58.3	56.1	55.8	55.0	54.1	52.5	49.6	49.5	47.8	47.3	47.1
99	VI-11	1554	34-34	127-45	2550	33.09	1023	57.8	60.0	60.8	60.6	60.6	60.6	60.6	59.0	56.3	54.5	54.7	54.7						
100	VI-11	1833	34-15	127-52	2520	---- ---	1023	59.0	63.0	61.7	61.3	61.3	61.3	61.3	60.6	57.6	55.8	54.9	53.8						
101	VI-11	2111	33-56	128-01	2430	33.24	1023	60.5	63.5	62.2	62.4	62.4	62.4	62.4	61.7	56.7	54.5	54.1	53.6						
102	VI-11	2332	33-40	128-07	2475	33.23	1023	60.5	64.0	62.6	62.2	62.2	62.2	62.1	61.0	56.8	54.7	53.4	52.5						
103	VI-12	0154	33-23	127-58	2350	---- ---	1023	62 0	65.0	62.4	61.9	61.9	61.9	61.9	60.6	59.5	57.2	55.2	54.5						
104	VI-12	0504	32-57	127-44	2400	33.08	1023	60.5	62.5	62.2	61.9	61.9	61.9	61.9	59.4	58.1	56.5	56.1	56.5						
105	VI-12	0903	32-30	127-30	2100	33.22	1023	59.0	63.0	62.8	62.4	62.4	62.4	62.4	61.2	60.1	59.0	57.9	58.8						
106	VI-12	1304	32-03	127-16	2325	33.49	1023	59.0	62.0	64.0	63.7	63.7	63.7	63.7	63.3	61.2	59.9	59.9	59.9						
107	VI-12	1532	31-45	127-07	2300	-------	1023	60.5	64.0	64.4	63.7	63.7	63.7	63.7	63.7	61.3	59.7	59.2	58.3						
108	VI-12	1706	31-37	127-02	--	33.43	1023	60.2	64.2	63.7	63.5	63.5	63.5	63.5	63.7	63.3	61.5	61.2	61.2	59.4					
109	VI-12	2001	31-54	126-52	2200	-------	1023	61.5	65.0	63.7	63.5	63.5	63.5	63.5	63.5	63.5	62.4	60.1	59.7						
110	VI-12	2259	32-10	126-43	2000	32.37	1023	61.0	64.0	63.7	63.5	63.5	63.5	63.5	62.8	62.1	61.3	60.8	60.1	58.1					
111	VI-13	0150	32-24	126-35	2380	-------	1023	60.0	64.0	64.0	62.4	62.4	62.4	62.4	61.9	60.1	59.7	58.8	58.1						
112	VI-13	0504	32-40	126-26	2330	33.50	1024	58.0	62.0	63.7	63.9	63.9	63.9	63.9	63.9	60.4	58.6	57.7	57.0						
113	VI-13	1302	33-01	126-14	2300	-------	1023	59.0	60.5	63.1	63.1	63.1	63.1	63.1	61.7	60.3	60.1	59.7							
114	VI-13	1614	33-23	126-03	2380	33.19	1023	60.5	62.5	61.9	61.9	62.1	62.1	62.1	62.6	61.2	60.4	60.4	59.0						
115	VI-13	1901	33-43	125-52	2370	---- ---	1021	62.0	64.0	61.3	61.3	61.3	61.3	61.3	61.2	59.0	58.6	57.2	57.9	55.6					
116	VI-13	2204	34-02	125-41	2500	33.10	1022	60.0	63.5	61.3	61.5	61.2	61.0	61.0	61.0	59.0	58.1	56.1	54.9						
117	VI-14	0106	34-18	125-30	2480	-------	1021	60.4	62.9	62.2	62.6	62.6	62.6	62.4	61.3	60.3	59.7	59.4	58.8	57.2					
118	VI-14	0403	34-34	125-20	2420	33.05	1021	58.5	61.0	60.4	60.6	60.6	60.6	60.6	60.4	58.3	57.7	57.4	55.4						
119	VI-14	0904	34-44	125-07	2450	-------	1019	58.0	61.0	59.9	60.4	60.6	60.6	60.4	60.3	56.1	54.7	54.0	53.6	51.3					
120	VI-14	1305	34-53	124-58	2400	33.12	1018	58.0	60.0	59.4	59.5	59.5	59.5	59.2	58.5	56.5	54.0	51.6	50.4						
121	VI-14	1633	34-42	124-43	2330	-------	1020	59.5	61.5	59.9	59.7	59.7	59.7	59.5	59.0	57.0	54.0	52.9	51.8						
122	VI-14	1904	34-27	124-30	2350	33.10	1020	61.5	67.0	60.6	60.6	60.4	60.3	60.3	60.1	58.5	57.6	57.2	56.5						
123	VI-14	2133	34-14	124-20	2350	---- ---	----	61.0	63.5	60.1	59.9	59.9	59.9	59.7	58.5	56.3	55.2	54.7	54.0						
124	VI-15	0001	33-58	124-09	2325	32.95	--	62.0	64.0	60.1	60.1	60.1	60.1	60.1	57.9	57.0	55.6	55.8	54.7						
125	VI-15	0237	33-41	123-56	2425	-------	1018	61.0	63.0	60.3	60.3	60 3	60.3	59.4	58.8	58.3	56.7	55.2	54.0						
126	VI-15	0504	33-25	123-45	2325	33.26	1019	59.0	60.0	59.7	59.7	59.7	59.7	59.7	59.4	57.0	55.9	55.2	54.9						
127	VI-15	0833	33-10	123-33	2175	-------	1019	59.0	61.0	60.1	60.1	60.1	60.1	58.8	57.2	56.1	55.4	54.1	53.6						
128	VI-15	1205	32-54	123-23	2300	33.26	1018	60.0	61.5	60.6	60.4	60.4	60.4	60.1	58.6	57.0	55.4	54.7	53.8						

TABLE 3—Continued

Summary of Observations at Bathythermograph Stations Occupied During the Albacore Survey, May 23 to June 18, 1960

Serial No.	Date	Time GMT	Location N. lat.	Location W. long.	Depth (fm)	Salinity ‰ (10M)	Barometer (mb)*	TEMPERATURE (°F.) Air Wet	Air Dry	Water Bucket (surface)	Bathythermograph (depth in feet) 0	30	50	100	150	200	250	300	330	400	490	500	600	655	700
129	VI-15	1431	32-41	123-12	2210	-------	1019	61.5	62.0	61.0	60.6	60.6	60.6	60.6	59.4	57.4	55.8	54.3	52.7						
130	VI-15	1703	32-26	123-00	2200	33.33	1019	61.0	62.0	61.5	61.2	61.2	61.2	61.0	59.2	58.5	56.1	53.8	52.5						
131	VI-15	1927	32-12	122-48	2325	-------	1019	62.0	63.0	61.5	61.5	61.5	61.5	61.5	60.3	58.6	56.5	57.2	55.8						
132	VI-15	2204	31-55	122-36	2240	33.25	1018	64.0	67.0	61.9	61.7	61.7	61.7	61.2	59.7	58.3	58.3	57.9	57.7						
133	VI-16	0034	31-39	122-23	1930	-------	1017	63.0	66.0	61.9	61.5	61.5	61.5	61.3	60.3	58.8	57.0	56.3	54.7						
134	VI-16	0402	31-16	122-06	2070	33.28	------	61.0	62.0	61.5	61.5	61.5	61.5	61.5	60.1	58.8	58.1	58.1	56.7						
135	VI-16	0632	31-00	121-54	2175	-------	1018	60.5	60.8	61.3	61.2	61.2	61.2	60.1	59.5	59.2	58.1	58.1	57.6						
136	VI-16	0801	30-50	121-48	2200	33.35	1018	60.0	61.0	62.2	62.1	62.1	62.1	61.2	59.9	59.0	57.7	57.4	56.5						
137	VI-16	1204	30-24	121-27	2150	33.40	1016	60.5	61.0	61.5	61.5	61.5	61.5	61.3	59.9	59.2	58.5	58.1	57.2						
138	VI-16	1431	30-09	121-16	2080	-------	1019	60.5	61.5	61.5	61.5	61.5	61.5	61.2	60.3	59.5	58.8	58.6	58.3						
139	VI-16	1633	29-55	121-05	1900	33.25	1019	61.5	62.5	62.1	62.1	61.9	61.9	61.7	61.3	59.9	59.2	58.5	58.5						
140	VI-16	1833	30-08	120-53	2120	-------	1019	62.0	64.0	61.0	61.0	59.7	59.7	59.2	58.1	57.0	56.3	56.1	55.4	54.7					
141	VI-16	2101	30-24	120-40	2000	33.44	1018	62.0	65.0	63.7	63.7	61.0	61.0	58.1	57.0	56.5	56.3	55.0	54.5						
142	VI-17	0002	30-39	120-27	2080	-------	1017	61.5	64.5	63.9	63.3	61.9	61.2	58.5	57.4	56.5	55.0	52.5	51.8						
143	VI-17	0337	30-57	120-13	2020	33.53	1017	59.5	61.0	62.2	62.1	60.8	60.4	60.1	57.0	56.1	52.9	52.3	51.3						
144	VI-17	0802	31-15	119-59	2050	-------	1018	58.5	59.5	60.3	60.8	59.9	59.7	57.7	57.2	55.9	55.2	54.5	54.0						
145	VI-17	1205	31-31	119-32	2050	33.43	1016	59.0	59.5	60.8	60.8	60.6	60.3	57.7	57.0	55.6	54.7	54.1	51.8						
146	VI-17	1503	31-47	119-32	1750	-------	1018	58.0	59.0	59.7	60.1	60.1	60.1	56.3	54.3	52.7	51.8	50.5	50.0						
147	VI-17	1804	32-04	119-18	830	33.71	1018	59.0	60.0	61.0	61.3	61.2	61.0	53.6	52.9	52.0	49.5	48.7	48.6						
148	VI-17	2114	32-21	119-01	410	-------	1016	61.5	63.2	61.3	62.4	61.3	59.9	58.3	55.2	52.0	49.8	49.1	48.9						
149	VI-18	0003	32-35	118-46	415	33.63	1017	60.0	61.5	62.8	63.3	62.2	61.9	57.0	55.0	52.0	50.9	49.8	49.5						
150	VI-18	0250	32-46	118-25	48	-------	1016	61.0	62.0	62.2	62.8	62.8	62.8	62.4	55.8	52.7									

compiled from California Cooperative Oceanic Fisheries Investigations (CCOFI) data, gathered within the California Current in the area of this cruise, show that temperatures have consistently run from 60 to 61 degrees F. and salinities from 33.20 to 33.30 parts per thousand. This suggests, at least through the period of the scouting cruise, that the albacore favored conditions associated with the California Current. Since the current is generally oriented from northwest to southeast parallel to the California coast south of San Francisco, the spring albacore migration may have been similarly oriented in 1960.

The lack of fishing response along the westernmost leg of the cruise (upper righthand limits of the temperature-salinity range in Figure 5) further indicates that the fish tended to migrate well within the confines of this water mass. This explanation is not, however, entirely consistent with the intimation by Yamanaka (1956), that albacore concentrations are linked with current boundaries. Trolling failed to yield a single fish in the transitional water at the western limit of the cruise area. Perhaps the boundary, as such, has become so mixed that the natural advantages of this type of region elsewhere are nonexistent off the coast of California.

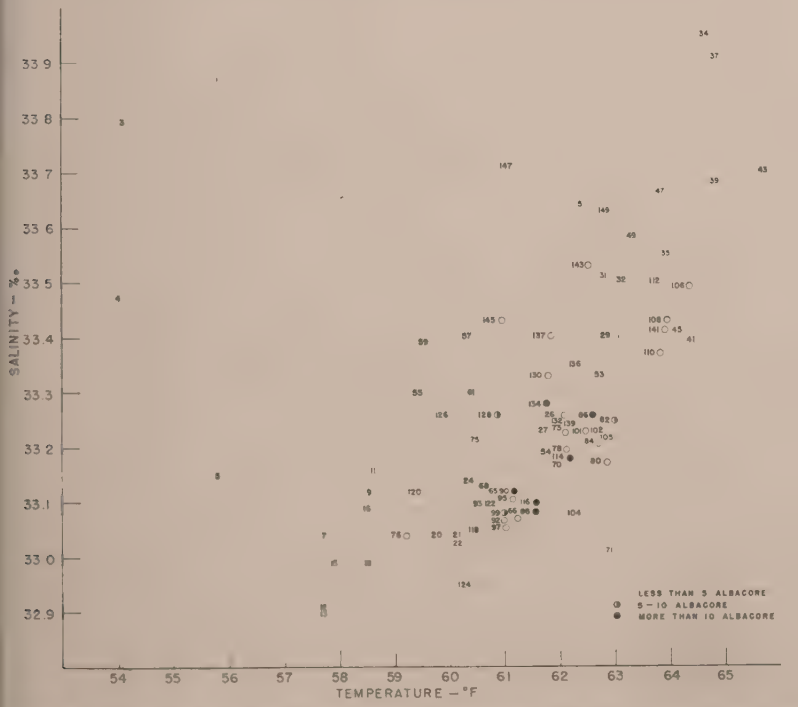


FIGURE 5. A temperature-salinity (T-S) diagram of the surface waters covered by the 1960 *N. B. Scofield* albacore survey. Arabic numbers indicate station numbers and are plotted to show the relationship between the two variables. Small circles indicate the relative position of albacore catches.

TABLE 4

Night-Light Observations Made During the Albacore Survey, May 23 to June 18, 1960

Date	Position		Summary of observations
	N. lat.	W. long.	
May 27	33° 29′	127° 48′	Approximately: 12 *Cololabis saira* (5-8 cm); 12 *Myctophum co forniense* (2-8 cm); 6 *Trachurus symmetricus* (40 cm)
28	31° 37′	128° 12′	A few *Cololabis saira* intermittently under the light
June 1	35° 21′	133° 20′	Only 1 or 2 *Cololabis saira* persisted under the light; 1 small myc phid and a large squid observed but not collected
3	37° 33′	133° 31′	A small ball of *Cololabis saira* persisted; colonial tunicates w abundant; 1 large squid observed
4	37° 55′	132° 06′	About 25 *Cololabis saira* persisted; several *Trachurus symmetric* colonial tunicates and 1 shark observed; 1 *Myctophum af* (35 mm) and 2 *Tarletonbeania crenularis* (23-24 mm) w collected
6	37° 05′	130° 38′	Only 1 small *Cololabis saira* observed
7	35° 23′	130° 36′	A single large *Trachurus symmetricus* observed
9	36° 40′	128° 08′	About 6 *Cololabis saira* persisted
10	34° 57′	127° 32′	Only 1 or 2 *Cololabis saira* observed

TABLE 5

Unusual Organisms Collected From Albacore Stomachs During the Albacore Survey, May 23 to June 18, 1960

Date	Location		Species
	N. lat.	W. long.	
June 7	35° 33′	130° 36′	*Lophotus* sp. (1) *Anotopterus pharao* (1)
8	35° 30′	129° 52′	*Anotopterus pharao* (1)
12	31° 48′	126° 55′	*Notolepis* (2) *Tetragonurus* sp. (1) *Vinciguerria nimbaria* (1)
15	31° 55′	122° 35′	*Icichthys lockingtoni* (1)

SUMMARY

1. The 1960 preseason survey of the northeast Pacific albacore fishing grounds was conducted from May 23 to June 18, 1960, by the Department of Fish and Game vessel *N. B. Scofield* (Cruise 60S3).

2. The oceanographic program was planned and co-ordinated jointly by the California Department of Fish and Game and the U.S. Bureau of Commercial Fisheries, Biological Laboratory, San Diego.

3. The area surveyed was bounded roughly by lat. 30° to 38° N., and long. 134° W. and the Channel Islands off California.

4. Surface trolling was used to locate albacore schools.

5. Except for one bigeye tuna the catch was entirely albacore. Of 153 landed 74 were tagged and released. At least an additional 50 albacore and five bigeye tuna were hooked but not landed.

6. Sea temperatures were measured from the surface to as deep as 700 feet and water samples for salinity determination were collected from approximately 33 feet (10 meters). Surface temperatures within the areas of catch ranged from 59.5 to 64.2 degrees F. and salinities from 32.95 to 33.53 parts per thousand.

7. The relationship between sea temperature and salinity indicated catches were restricted to the water mass of the California Current system.

ACKNOWLEDGMENTS

Many people contributed to the success of this cruise. Most notable among these, from the California State Fisheries Laboratory were Robert R. Bell who assisted in the field, and particularly Captain Richard B. Mitchell and the crew of the *N. B. Scofield*. From the San Diego Biological Laboratory, Mr. James H. Johnson co-ordinated cruise planning and data processing and Donald C. Greenland assisted materially in making the collections at sea.

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SURVIVAL AND GROWTH OF LARVAE OF THE EUROPEAN OYSTER, O. EDULIS, AT LOWERED SALINITIES

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The European oyster, *Ostrea edulis,* in its native habitat, is found primarily in oceanic or nearly oceanic salinities. Its native range extends from the southern coast of England and the Scandinavian countries to the Mediterranean, but recently it has been successfully introduced into New England waters (Loosanoff, 1951, 1952, 1955; Welch, in press).

Initially, Loosanoff (1955) proposed this oyster for introduction into those areas where the summer water temperatures rarely, if ever, are high enough for American oysters to reproduce. More recently, because of heavy mortalities of American oysters in several states, he has suggested that *O. edulis* might be introduced as a second commercial oyster into these and other oyster-producing areas of the United States. Since European and American oysters belong to different genera, they will not interbreed and, what could be extremely important, European oysters might not be susceptible to some of the diseases now affecting American oysters. Moreover, since European oysters are larviparous and their larvae are usually 175 μ to 185 μ at the time of release, the food requirements of the larvae are not as restricted as those of the young larvae of American oysters. Therefore, good sets of European oysters might frequently be obtained in seasons when setting of American oysters fails.

Korringa (1941) reviewed the literature on the effects of salinity on eggs and larvae of several species of oysters, including *O. edulis.* He found no correlation between rate of growth of larvae or intensity of their setting and differences in average salinities in the Oosterschelde, Holland, ranging from 25 to 35 ppt. He quotes the assumption of Gaarder (1932, 1933) and Gaarder and Bjerkan (1934) that 24 ppt is the lowest salinity for satisfactory growth of larvae of *O. edulis.* Korringa also states that changes of salinity, within the range found in the Oosterschelde, cannot be held responsible for the success or failure of spatfall of *O. edulis* in this area, and points out that experiments *in vitro* had not yet been carried out to determine the effect of salinity upon setting.

Walne (1956) reported experiments on rearing *O. edulis* larvae in salinities initially adjusted to 21.1, 25.9, 27.9 and 31.3 ppt. The water in the larval cultures was not changed during the course of his experiments and, apparently due to evaporation and the addition of algal food suspension, the salinity in all cultures increased. Thus, in cultures initially at 21.1 ppt the salinity increased to 25.9 and 26.2 ppt. Under these conditions he found that the larvae survived and grew

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throughout the salinity range tested, but he did not obtain any spatfall in the cultures started at 21.1 ppt.

The present study was undertaken to obtain more precise data on the effect of low salinities on egg production and incubation in *O. edulis,* upon survival and growth of larvae, and upon setting of mature larvae. Since several of the oyster-producing areas in the United States, where we might wish to introduce *O. edulis,* are characterized by relatively low salinities, such information is necessary.

Methods

The methods employed were essentially the same as those used by Davis (1958) in a similar study of the salinity tolerance of eggs and larvae of the American oyster. However, since *O. edulis* is larviparous, to obtain larvae from these oysters it was necessary to hold adults in aquaria during the period of gonad development, spawning and incubation. Approximately ten adult oysters were kept in each aquarium in 60 liters of water. One group of oysters was kept at our normal salinity (27 ppt); another group was kept at a salinity of 20 ppt; and a third group was kept at 17.5 ppt. We used sea water, filtered through an Orlon filter designed to remove particles above 15 μ in diameter, and lowered the salinity to the desired level with demineralized tap water. Water in these aquaria was changed daily and three to four liters of algae were added during each change to supplement the food present in the water.

The adult oysters kept at normal salinity provided the larvae used in these experiments. As soon as larvae were noticed after release, they were collected by draining the water from the aquarium through a 250-mesh screen. By using care to drain without disturbing the sediment on the bottom of the aquarium, healthy larvae were collected relatively free of debris. These larvae were then resuspended in a three-liter Pyrex jar, the number of larvae per ml. determined, an appropriate volume pipetted into each of a series of one-liter polyethylene beakers, and the volume made up to one liter of the desired salinity. Two beakers of larvae were set up at each of the following salinities: 27 ppt (control), 25 ppt, 22.5 ppt, 20 ppt, 17.5 ppt, 15 ppt, 12.5 ppt and 10 ppt.

In the first experiment we used 6400 and in the second, approximately 13,000 larvae per beaker. Following the procedure of Davis (1958), to hold salinities constant, the one-liter cultures received food only every second day when the water was changed, instead of daily as is the usual practice. All the cultures were covered to prevent excessive evaporation and kept in a constant temperature bath at 23° C. ± 1° C.

In the two experiments to determine the effect of low salinities on setting of mature larvae, we reared the larvae in 15-liter culture vessels at 27 ppt until their average size was 250 μ and many were already in the 275 to 300 μ range. Approximately 9000 of these larvae were pipetted into each of a series of one-liter beakers filled with water adjusted to the desired salinities. In the first experiment, because of the limited number of mature larvae available, we used a single culture at each salinity, but in the second, mature larvae were abundant and duplicate cultures were used at each salinity.

A single oyster shell in each beaker was used as cultch. These shells were replaced every second day, as the water was changed, and the shells removed

were examined under a dissecting microscope to determine the number of spat caught. Only those setting on the smooth, white, inner surface of the shell were counted. Since many oysters also set on the rough, dark, outer surface of the shell, on the walls of the container, and on small shell fragments or other debris where it is impossible to count, the number of spat recorded is only a rough index of the total number setting.

Results

Effects of lowered salinities on growth of larvae

The results of the first experiment showed that growth of larvae was virtually normal in salinities as low as 22.5 ppt (Fig. 1). At 20 ppt, although larvae grew

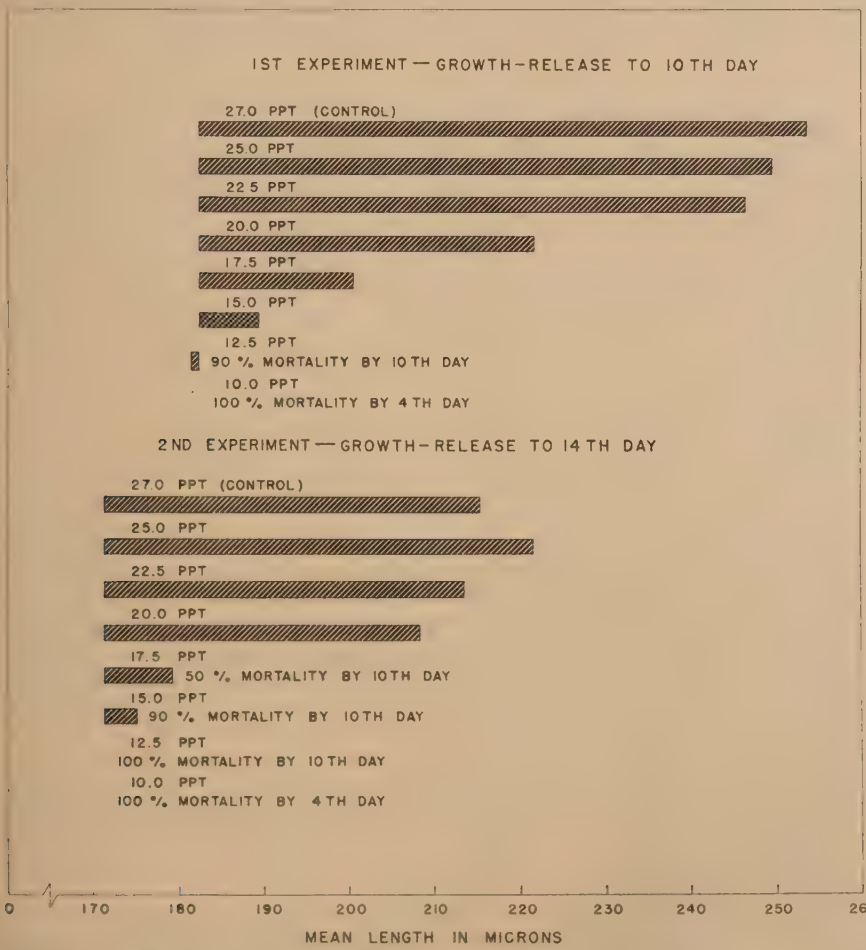

Figure 1. Growth of *O. edulis* larvae at different salinities. Mean lengths are based on measurements of 100 larvae from each of duplicate cultures at each salinity.

at a considerably slower rate, some were reared to setting stage and metamorphosed. At 17.5 ppt growth was extremely slow; no larvae reached the setting stage and eventually all died. At 15 and 12.5 ppt, growth of larvae was even slower, but some lived at each salinity for ten days or more. Larvae kept at 10 ppt all died within four days.

The larvae used in the second experiment were about 11 μ smaller at the time of release and grew at a considerably slower rate than those used in the first experiment (Fig. 1). Since larvae from the brood used in this second experiment grew normally in other cultures set up at the same time, we believe the slower growth was the result of the higher concentration of larvae (13,000 per liter as opposed to 6000 per liter in the first experiment). This would indicate that to assure good growth these larvae must be kept in much lower concentrations than larvae of either *Venus mercenaria* or *Crassostrea virginica,* both of which grow quite well at 13,000 individuals per liter.

TABLE I

Effect of reduced salinities on setting of larvae reared almost to setting stage at 26–27 ppt

Salinity in parts per thousand	Average number of spat per culture	
	1st experiment	2nd experiment
26–27 (Control)	147	134
25.0	504	145
22.5	120	171
20.0	114	38
17.5	24	5
15.0	4	0.5
12.5	0	0
10.0	0	0
7.5	0	0

The pattern of growth was generally the same in both experiments, even though growth of larvae was much slower in the second experiment. Growth of larvae was not greatly different from that in control cultures at salinities of 20 ppt and higher. As in the first experiment, the rate of growth dropped off sharply between 20 ppt and 17.5 ppt. Mortality was high and growth negligible at all lower salinities. Because of the very slow growth of larvae, the second experiment was discontinued before larvae in any of the cultures reached setting stage.

Effects of lowered salinities on setting

Two experiments were run to determine the minimum salinity at which larvae of *O. edulis* could set. In both, larvae that had been reared almost to metamorphosis at our normal salinity of 26–27 ppt were transferred directly to lowered salinities and their setting recorded (Table I).

Although a salinity of 20 ppt was the lowest at which larvae could be reared from release through metamorphosis, some mature larvae transferred to salinities of 17.5 and 15 ppt did set (Table I).

It is significant that all of the set obtained at 17.5 and 15 ppt occurred within four days after the larvae were transferred to these salinities, while setting continued for as long as 14 days in higher salinities. This indicates that only those larvae that were almost ready to set at the time of transfer were able to complete growth and metamorphose at these lower salinities, while all less developed larvae died. However, even those larvae that were ready to set at the time of transfer were unable to complete the process of metamorphosis at salinities of 12.5 ppt or lower.

A similar record of the number of set obtained from larvae reared at lowered salinities showed that while there was no significant mortality within ten days in a salinity of 15 ppt nor in any of the higher salinities, none of the larvae grown at 15 and 17.5 ppt survived to set. Even in cultures kept at 20 and 22.5 ppt, significantly fewer larvae succeeded in completing metamorphosis than in cultures reared at 25 ppt or in control cultures.

Effects of lower salinities on gonad development, spawning and incubation

Because it was found (Davis, 1958) that eggs from *C. virginica* that had developed gonads at salinities of about 8.75 would develop into straight hinge larvae at considerably lower salinities than would eggs from parents that had developed gonads at 26–27 ppt, we thought it worth while to attempt to induce gonad development, spawning and incubation of *O. edulis* at lowered salinities. We hoped to use larvae from oysters kept at salinities of 20 ppt and 17.5 ppt in salinity experiments parallel with those on larvae from oysters kept at our normal salinity, to determine whether the salinity tolerances of the larvae were altered by the salinity in which the parent oysters had developed gonads and spawned.

The adult *O. edulis* that were kept in aquaria at 20 ppt and at 17.5 ppt failed to release any normal living larvae. In other respects, however, transfer to these lowered salinities appeared to affect them for only a short time. Oysters transferred to 17.5 ppt, for example, failed to feed normally for only a few days, but thereafter cleared the water of the algae added as food, as did those kept at higher salinities. These oysters were kept in these salinities for 60 days and appeared normal in every respect, except that they produced no normal larvae.

Evidence of spawning of at least one female, in the group kept at 20 ppt, was observed, but no living larvae were recovered. A few empty larval shells were found on several occasions, but there were not enough of these to account for a normal brood from a single female. Although spawning was not observed in the group kept at 17.5 ppt, on several occasions highly abnormal living larvae were recovered. These larvae either had no shells at all or had small, highly abnormal ones. Nevertheless, many of them were capable of taking food and lived for several days after transfer to normal sea water. Because there were only a few of them, their further development could not be followed.

Discussion

The results of our experiments indicate that culturing of *O. edulis,* in areas where the salinity is 20 ppt or lower, cannot be successful because these salinities are too low for reproduction of this species. It is possible, nevertheless, that in

situations where there is a gradation of salinities, mature larvae, developing and growing to setting size at salinities of about 22.5 ppt or higher, could be carried by currents to salinities as low as 15 ppt and set and grow there.

Since some of the larvae reared at 20 ppt did metamorphose, it is possible that culture of *O. edulis* at this salinity might be successful, but growth of larvae would be slow and the intensity of setting reduced. Moreover, adult oysters kept at this salinity failed to give any living larvae. While it is possible that we might have had different results if we had used more oysters, the number of oysters (only 10) kept at this salinity was the same as the number kept at our normal salinity that released the several million larvae used in these experiments.

The release of abnormal veligers by oysters kept at 17.5 ppt is, we believe, positive evidence that this salinity is too low for normal larval development. It is possible that oysters acclimated to this salinity over a longer period of time might have given viable larvae. However, the results of Davis (1958) showed that keeping adult American oysters, which had developed gonads at 8.75 ppt, for only a few days at salinities of 7.5, 10 and 15 ppt altered the salinity tolerance of their eggs.

Previous investigators using, for the most part, field data have shown that *O. edulis* larvae can grow and set at salinities as high as 34 to 39.5 ppt (Mazzarelli, 1924). Korringa (1941) also states that, "It is my opinion that variations in salinity between 25 ppt and 35 ppt probably have little or no influence on larval growth and development in *Ostrea edulis*" (pp. 133–134).

Our results cannot be compared directly with those of Walne (1956) because he did not change the water and his salinities were not held constant. Using our methods, however, larvae were reared to metamorphosis and some set was obtained at salinities of 20 and 22.5 ppt, both lower than the lowest initial salinity (25.9) from which Walne obtained spatfall.

Our results confirm Korringa's opinion that a salinity of 25 ppt has no appreciable adverse effect on growth of larvae. They further show that the lower limit for good growth and setting is about 22.5 ppt, although larvae can grow to metamorphosis at 20 ppt and mature larvae can set at even lower salinities.

The authors wish to express their appreciation to Dr. V. L. Loosanoff, Director of Milford Laboratory, for suggesting the problem and editing the manuscript, to Mr. Herbert Hidu for assistance in caring for the cultures and making many of the measurements, to Mr. Manton Botsford for preparing the figure, and to Miss Rita Riccio and her staff for their care in editing and preparing the manuscript. Thanks are also given to the John Murray Committee of the Royal Society for the travelling grant to one of us (A. D. A.) which made this cooperation possible.

Summary

1. At salinities of 25 and 22.5 ppt growth of larvae of *O. edulis* and intensity of setting was not significantly different from that in control cultures at our normal salinity of 26–27 ppt.

2. At 20 ppt growth of larvae was appreciably slower than at higher salinities and the intensity of setting was reduced.

3. At 17.5 and 15 ppt larvae lived for some time and showed appreciable growth, but they all died prior to metamorphosis.

4. At 12.5 ppt larvae showed no growth and by ten days after swarming they had suffered 90% or higher mortality.

5. At 10 ppt all larvae died in less than four days.

6. Some larvae that had been reared to setting size at a salinity of 26–27 ppt were capable of setting in salinities as low as 15 ppt.

7. No normal larvae were obtained from adult oysters kept at salinities of 20 or 17.5 ppt.

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Second Joint Meeting: California Branches of the American Meteorological Society

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e U. S. Naval Postgraduate School at Mon-, Calif., played host to the second statewide ring of California meteorologists on 13 and pril 1962. The meeting encompassed both ssional and social functions, with meteoro-l sessions on Friday and social activities on y evening and Saturday. Registered at-nce at the Friday sessions totaled 85 persons ling representatives from AMS Branches in an Francisco Bay Area, Sacramento, Santa ara, Los Angeles and San Diego, and from Postgraduate School. Kenneth C. Spengler, utive Secretary, and Prof. Morris Neiburger, President, attended as invited guests.

e event met with a high degree of success argely to the capable and energetic efforts of E. T. Harding, Officer in Charge of Me-logy Curricula at the School, who handled gements for the meeting facilities and social ities. The latter featured a cocktail hour on vening of the 13th, followed by a banquet and entertainment, ending with the mellow strains rbershop singing around the piano.

e program was organized by Hal Root, as-l by Larry Eber. It comprised a morning on for technical papers and an afternoon ses-on topics of special interest to California me-logists. A luncheon was held Friday noon ring an address by Prof. Neiburger on prog-and plans of the Society.

the morning session, which was chaired by Root, the following papers were presented:

Southern California rainstorm of December 60. Lcdr. Carl Blaes, Fleet Weather Fa-ity, San Diego, Calif.

ystematic approach to presenting mesoscale ta. Clement J. Todd, Meteorology Research, c., Altadena, Calif.

lane instrumentation for National Science oundation storm study. John W. Flavin, Jr., erometric Research, Inc., Goleta, Calif.

Investigation of parameters relating to winter fog dissipation in the Central Valley. Major Bill Trevorrow, Mather AFB, California.

Current status of the Fleet Numerical Weather Facility operations and research. Cdr. Wolff, FNWF, Monterey, Calif.

Dr. Arnold Court (formerly Northern California Branch) came from Massachusetts to serve as chairman and moderator for the afternoon sessions. Although stimulated by local and regional interests, the subjects bear implications of more general importance. A summary of the discussions is given below.

Topic 1. Instrumented offshore weather buoys

While lacking the spectacular appeal of satellites, the development of unmanned instrumented, deep-ocean buoys is being hopefully watched by many people concerned with marine meteorology and oceanography. Cdr. Frederick G. Robinson, USN (San Diego Branch), who was the principal contributor in this discussion, described the work the Navy is doing in testing two types of buoys currently undergoing development. One of these is the NOMAD which has been tried with success in the Gulf of Mexico, having survived two hurricanes. The second type is the Naval Research Laboratory (NRL) buoy, originally designed as free floating, but now being tested as a deep-anchored buoy. One of these buoys (NRL) was anchored approximately 20 miles southwest of San Nicolas Island on 13 April 1962. This was primarily a deep water mooring test but telemetered reports of pressure, wind and temperature have been obtained. Further tests will continue with a mooring in 2000 fathoms of water, planned for early August. It is believed that the data obtained on mooring, observing and telemetering techniques will make possible, in the not too distant future, the design and construction of a buoy which will be light in weight, reasonable in cost

and operationally capable of providing the data which meterologists and oceanographers so urgently require.

Although far-reaching plans have been proposed for extensive networks of oceanic buoys, Cdr. Robinson reiterated that before this can be achieved, many formidable obstacles must yet be overcome. These include problems of anchoring, instrumentation, timing and telemetering of data, and loss of buoys due to accidental damage or theft.

He noted that with existing instrumentation, the NOMAD and NRL buoys would be, almost exclusively, meteorological tools. However, oceanographers are keenly interested in devising means of obtaining a wide variety of subsurface measurements from buoys. In particular, he called attention to a working committee of the Eastern Pacific Oceanic Conference, which is presently conducting a series of meetings to assess the needs, transmission problems, aspects of data handling, and instrumentation problems connected with buoy utilization for both meteorology and oceanography.

Topic 2. Inter-branch coordination and relationship with the national society

Dr. T. B. Smith, (Los Angeles Branch) led off discussion of this topic by noting that a growing diversity of interests and disciplines is occurring within the meteorological profession. A direct consequence of this tendency toward specialized interests is a general decrease in communication between members of the society engaged in the different disciplines. The effects at the local level have been to weaken the strength and vigor of the branches. Typical members of a local chapter now appear to have considerably less in common, professionally, than was the case five or ten years ago. In attempting to bridge the gaps, local programs have often been too broadly popularized, with the result that many members fail to attend sessions they find lacking in substance. Dr. Smith feared that this category of members includes those creative leaders in the field who could provide the greatest stimulus at the local level. He suggested that there needs to be a re-evaluation of the function of the local chapter and its relation to the national society.

There are, for instance, a number of meteorological activities and problems which are of common interest to the five California Branches of the AMS. These include (in addition to other topics covered at this meeting) the development of state policy on weather-dependent problems, such as air pollution and weather modification, the encouragement of Loomis School-type s mer high school programs for the western st

In regard to relations with the National ciety, Dr. Smith observed that only a small nun of individuals in each local chapter are actively terested in affairs of the national group, and these individuals feel a need for a more adeq mechanism to express themselves on nati problems.

He pointed out, as an approach to this situa and also to the interbranch problems mentic earlier, the value of a regional group, such as California organization. Such a group offe means for interested members of the constitu branches to meet for discussion of mutual p lems. By reporting the results of such discuss at individual branch meetings, greater interes the problems may be generated. Moreover, regional group can be instrumental in strengt ing communication with the national body.

Einar Hovind (Santa Barbara Branch) gested that communication between the nati council and AMS members might be enhance council seats were filled on a basis which w provide better geographical representation. Sp ing further, on public relations at the nati level, he suggested that the AMS Statement Policy, which are released from time to time, c be issued with more assurance as considered o ions of the meteorological profession if the A members had prior opportunity to examine t and submit comments.

Professor Neiburger expressed the belief the caliber of the council members is very and that little bias exists as a consequence of proportionate geographical representation. explained that the policy of the nominating c mittee in selecting candidates is to get broad resentation from different organizations and gr (such as Air Force, Navy, Weather Bureau, versities, etc.) and to get people with ability interest in Society affairs.

In regard to AMS policy statements, Profe Neiburger noted that such statements either o nate or are referred to a committee whose m bers are familiar with the subject of the staten under consideration. Generally, he believed competence of the committee and the council t adequate to insure that released statements well considered and valid. However, as a co quence of having to satisfy various viewpoints, statements tend to be less specific than they m be otherwise. He suggested that one way branches to participate more directly in this

would be to propose, from their own groups, duals to serve on the committees.

consequence of the discussions, it was agreed he joint meetings of California Branches profitable and should be continued on an an- basis. Further, that the coordinating com-, composed of representatives from each h, should play a more active role in the fu- for instance, by focusing attention on prob- for joint consideration. In particular, Ar- Court emphasized the need for an organized recognized as representing California me- ogists, which could tender advice or recom- ations to state agencies on problems with me- ogical implications.

was determined, subsequently, that Einar nd would be program organizer for the next meeting.

c 3. Development of mesoscale meteorol- gy in California

ment J. Todd (Los Angeles Branch) opened iscussion with an outline of key questions: Who needs mesoscale meterology in Cali- ? (b) What sort of mesoscale networks at present? (c) How can the results be made ble to users? (d) To what extent are cen- ed analyses feasible or desirable?

noted that existing networks include forestry, ollution, airways, water resources, agricul- and radar systems.

dd Crawford (Sacramento Branch) ampli- on agricultural needs, stressing local wind asts (for application of insecticides, etc.) and short-range rain or moisture forecasts.

bert Weaver (Sacramento Branch) noted major forestry problem is the measurement e hazard attributable to weather effects and ibed the Wildland Fire Danger Rating Sys- eveloped for California to deal with this prob- The Fire Danger Rating System is based 5 Danger Rating areas, in which there are re-weather stations. The observing stations naintained by a number of organizations, in- ng the U. S. Forest Service and the California ion of Forestery (only one is a Weather Bu- station). From data collected at the report- tations, predictions of Fire Danger Rating es are made for each rating area to assist in ontrol. Increased accuracy of predictions is sought by increasing the number and con- ntly reducing the size of the U. S. Weather au Fire Weather forecasting districts and y issuing morning and afternoon fire weather asts. Weather data from all the 335 fire- weather stations is being processed through an IBM 704 (later a 7090) computer program. The resulting 10-yr normals and averages will be used both as forecasting aids and as operational planning tools.

Sidney Frank (Santa Barbara Branch), referring to mesoscale studies of the marine layer in the Santa Barbara Channel, observed that they were facilitated by the cooperation of several groups, engaged in local investigations and having overlapping interests and interlocking data, and that this appears to be characteristic of many mesoscale endeavors. He posed the question of how this cooperative approach, which is geared to specific problems, fits into the concept of standardized meso systems.

Hal Root (Northern California Branch) mentioned that a new cooperative "mesoscale" group has been organized by Dr. Al Miller of San Jose State College to draw together people interested in meteorology of the San Francisco Bay Area. This group is compiling a list of observing stations in the area and also a bibliography on Bay Area meteorology.

Roy Endlich (Northern California Branch) called attention to mesoscale features of circulation in the free atmosphere, particularly those arising from local orographic influences. He noted that there are observational tools in California, such as radar and aircraft which, if utilized more fully, would enable the collection of data needed to investigate this problem.

Mr. Root expressed the opinion, based on experience with TIROS, that satellite pictures should be of considerable value in the mesoscale problem by revealing local and small-scale circulation patterns not otherwise detected.

Discussion of the topic was concluded with some comments on the difficulties of coordinating mesoscale activities and making the data available to interested users. Mr. Todd asked for consideration of a national AMS meeting on mesoscale meteorology.

Topic 4. Improving the presentation of technical papers

This topic was introduced by Elmer Robinson (Northern California Branch) who drew attention to the substantial cost involved in a meeting, such as this one, in terms of the time of those attending. If a speaker delivering a technical paper does not present his material effectively, this time is clearly not being profitably spent. Mr. Robinson stressed the concept of "audience consideration" as an essential key to good presentation. He suggested

that the AMS might work up guidelines to aid in the preparation and delivery of papers.

In the discussion which followed, distinction was made between quality of material and quality of presentation. Opinions both pro and con were registered as to whether papers should be screened more carefully when the program is being drawn up. Opinion was also divided on what proport of responsibility the speaker and presiding ch man each must assume for over-running t limits.

No one contested the positive value of ef spent to achieve efficient organization and l presentation of technical and scientific papers.

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Blue Crab Movement in Coastal South Carolina, 1958–59

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U. S. Bureau of Commercial Fisheries, Beaufort, North Carolina

ABSTRACT

In 1958 and 1959, 4,353 blue crabs of 5 inches or greater carapace width were tagged in three estuaries and at two coastal locations in South Carolina to determine coastal movement. Locations of 530 returns indicate that most of the crabs did not migrate between estuaries, but limited their movement between the lower estuary and adjacent coastal waters. It was concluded, at least for South Carolina, that management measures can probably be confined to individual estuarine systems rather than large coastal regions.

INTRODUCTION

The blue crab, *Callinectes sapidus*, fishery the Atlantic and Gulf coasts of the United tes is limited to areas where crabs are ıcentrated, and, therefore, knowledge of ir movement is important for management. e purpose of this investigation was to de- mine movement of blue crabs in coastal ıth Carolina, and to consider possible nagement implications. This was a co- erative study by the Bears Bluff Labora- ies, Wadmalaw Island, South Carolina, l the U. S. Bureau of Commercial Fisher- Beaufort, North Carolina.

Studies in Chesapeake Bay indicated that b migrations are related to phases of the cycle (Churchill, 1919; Fiedler, 1930; iitt, 1939). Spawning begins in the spring l continues throughout the summer in high inity waters adjacent to the inlets and an. After hatching, larval or young crabs ve to less saline waters of sounds and riv- where they mature in about one year. nale crabs mate after their last molt, and n move to more saline waters to spawn. les tend to remain in brackish waters. idies in Delaware Bay (Porter, 1956), in xas (Daugherty, 1952), and in Louisiana arnell, 1959) at various times during the ır indicated movement of adult crabs in se areas similar to that in Chesapeake Bay. hough the life history of the blue crab in ıth Carolina has not been studied it is . probably quite similar in all sections of coast" (Pearson, 1951).

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METHODS

In 1958 and 1959, 4,353 crabs of commercial size (5 inches or greater in carapace width) were tagged and released in South Carolina waters. Crabs were captured by otter trawl, tagged, and released in the vicinity of capture. All females were mature, but maturity of males could not be determined by observation.

A carapace tag (Rounsefell and Everhart, 1953) was attached to each crab with stainless steel wire. One side of the tag was numbered, and the other bore the name and address of the tagging institution and a reward notice. Reward for each tag returned was 25 cents, and recoveries were dependent on voluntary returns. Publicity was given the project through newspapers and reward posters displayed by crab dealers and processors.

Tagging was done in three estuaries and two coastal areas. The estuaries were the North Edisto River at Point of Pines, the Ashley–Cooper River at Mt. Pleasant, and Bull Bay off Five Fathom Creek. Coastal tagging was done near the North Edisto River sea buoy 4 miles from the mouth of the estuary, and off Morris Island ¾ mile from the mouth of the Ashley–Cooper River (Figure 1).

In 1958, 1959, and 1960, 530 tags were returned, mostly by commercial fishermen. Eighteen lacked sufficient recovery information and were not used in the analysis. Tagged crabs were caught by pot, trotline, and otter trawl. These gears were fished most of the year in sounds and bays, but trawls were also operated in coastal waters at the mouths of rivers and along ocean beaches. It was assumed that tagged crabs were similar in behavior to untagged crabs. Although

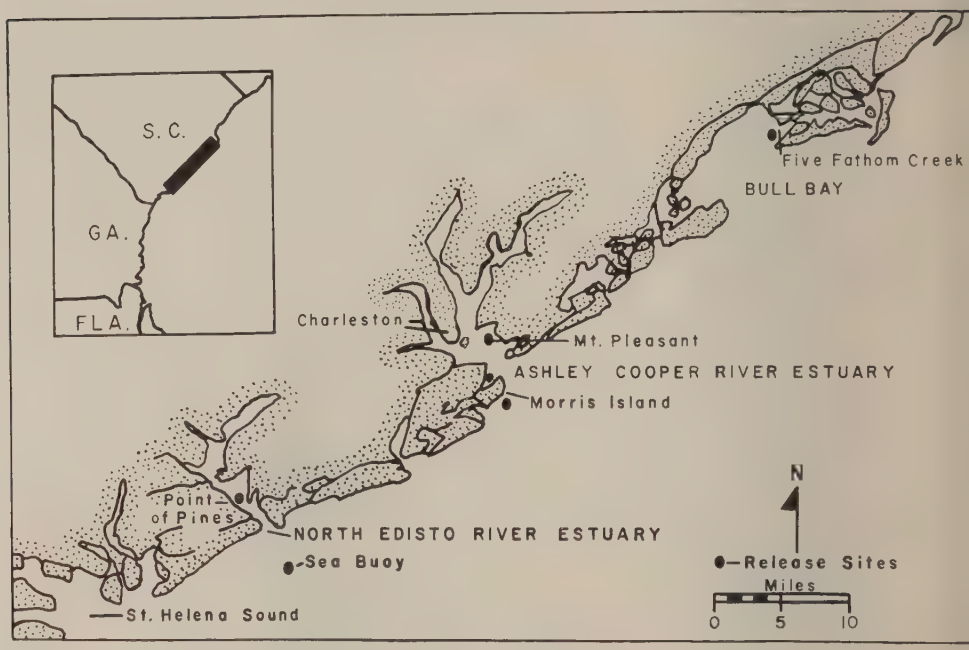

FIGURE 1.—Blue crab tagging locations, South Carolina, 1958–59

fishing effort was not uniform throughout the coastal area, this was not believed to have materially affected conclusions regarding crab movement.

RESULTS

Of the 2,918 crabs (1,612 males, 1,306 females) tagged within estuaries, 409 (229 males, 180 females) were recovered (Table 1). Sixty-five percent of the male and 40 percent of the female recaptures were within the area of release. Area of release was de fined as within the estuary, but not mor than 5 miles from the tagging location. Thre percent of the male recaptures were mad outside the release area in the estuaries up river from the tagging location.

Twenty-nine percent of the male and 5 percent of the female recaptures were i coastal waters outside the estuaries. Most re coveries (79 percent) were made less than

TABLE 1.—*Recovery of tagged blue crabs released in estuarine waters of South Carolina*

Location and date	Number released		Number recovered									
			Release estuary				Outside release estuary					
	Sex		Release area		Outside release area		Coastal waters		Other estuaries		Total	
	M	F	M	F	M	F	M	F	M	F	M	F
North Edisto River:												
Point of Pines												
January 1958	878	610	82	18	3	–	58	91	–	5	143	11
January 1959	208	12	23	–	1	–	4	–	6	–	34	
March 1959	11	11	2	–	–	–	1	–	–	–	3	
August 1959	13	1	1	–	–	–	–	1	–	–	1	
Ashley-Cooper River:												
Mt. Pleasant												
March 1959	223	257	4	1	2	–	–	6	–	1	6	
Bull Bay:												
Five Fathom Creek												
March 1959	279	415	37	53	1	–	3	4	1	–	42	5
Totals	1,612	1,306	149	72	7	–	66	102	7	6	229	18
Percentages	–	–	65	40	3	–	29	57	3	3	100	10

TABLE 2.—*Month and area of recovery for 251 tagged blue crabs released near Point of Pines in the North Edisto River in January 1958 and recovered from January–August 1958*[1]

Month	Recovery area					
	Vicinity Point of Pines		Vicinity sea buoy		Other coastal areas	
	M	F	M	F	M	F
January	–	–	–	–	–	–
February	–	–	–	–	–	–
March	1	–	22	25	1	–
April	23	2	29	24	–	3
May	35	2	5	10	–	7
June	21	11	–	7	1	11
July	2	1	–	2	–	4
August	–	–	–	–	–	2
Totals	82	16	56	68	2	27
Percentages	59	15	40	61	1	24

[1] Not included in the table were three recoveries made away from estuary after August 1958 and three made upriver from Point of Pines.

miles from the mouths of the estuaries where tagged. Four males and 31 females were recovered in coastal waters more than 5 miles from the estuaries. Seven males and six females (3 percent of the recoveries) were recaptured in other estuaries. These studies indicate that a greater percentage of females moved from the estuaries to coastal waters than did males, and that most crabs leaving the estuaries remained in adjacent coastal areas.

Tagging in the North Edisto River at Point of Pines in January 1958 indicated that some crabs moved from the estuary to coastal waters in late winter, and that a greater percentage of females remained in coastal waters in the spring and summer than did males (Table 2). A smaller proportion of crabs moved to the area of the North Edisto River sea buoy from Point of Pines in late winter of 1959 compared to that of 1958 (Table 1). From January to March 1958, and to a lesser extent in 1959, water temperature and salinity near Point of Pines were generally lower than near the sea buoy.[3] Crab movement in late winter from Point of Pines to the warmer and more saline waters in the vicinity of the sea buoy, particularly in 1958, may have been related to these environmental factors.

Of the 1,435 blue crabs (500 males, 935 females) tagged in coastal waters, 103 (44 males, 59 females) were recovered (Table 3). Thirty-nine percent of the male and 47 percent of the female recaptures were in the area of release. Area of release was defined as coastal waters within 5 miles of the tagging location.

Fifty-two percent of the male and 34 percent of the female recoveries were made in estuaries. Almost all recoveries were in the estuary adjacent to the coastal tagging site. Only four males and four females were recovered in other estuaries. Nine percent of the male and 19 percent of the female recoveries were made in coastal areas more than 5 miles from location of tagging. In general, crabs tagged in coastal areas remained in the area of tagging or moved into the adjacent estuary. More males than females moved from coastal waters into estuaries, and more females than males were recovered from coastal waters at distances greater than 5 miles from location of tagging.

From all experiments, 71 crabs (19 males, 52 females) or 14 percent of those recovered were recaptured away from both estuarine and coastal tagging locations. Thirty-three recoveries were made north and 38 recov-

[3] Unpublished data, Bears Bluff Laboratories, Wadmalaw Island, South Carolina.

TABLE 3.—*Recovery of tagged blue crabs released in coastal waters of South Carolina*

Location and date	Number released		Number recovered							
	Sex		Release area		Outside release area				Total	
					Estuarine waters		Coastal waters			
	M	F	M	F	M	F	M	F	M	F
North Edisto River:										
Sea buoy										
January 1958	5	55	–	6	–	2	–	1	–	9
March 1959	70	106	4	9	7	2	2	1	13	12
August 1959	202	398	2	1	12	9	2	2	16	12
Ashley-Cooper River:										
Morris Island										
March 1959	58	182	4	5	2	2	–	4	6	11
August 1959	165	194	7	7	2	5	–	3	9	15
Totals	500	935	17	28	23	20	4	11	44	59
Percentages	–	–	39	47	52	34	9	19	100	100

eries were made south of the release areas. Distances of outside recoveries from release areas were: 33 crabs, 5 to 15 miles; 29 crabs, 15 to 30 miles; 7 crabs, 30 to 50 miles; 1 crab, 90 miles; and 1 crab, 145 miles. The last recovery, a female tagged in January 1958 in the North Edisto River, was recaptured in May 1958 near the mouth of the St. Johns River, Florida. The most distant recovery of a male was 30 miles from location of tagging.

CONCLUSIONS

These studies indicate movement of adult crabs between the lower estuary and adjacent coastal waters. Only 3 percent of the tagged crabs recaptured were recovered in estuaries other than those in which tagged. Random coastal movement was demonstrated by a small percentage of crabs. In general, commercial-sized crabs did not migrate between estuaries, but limited their movements to the estuary or adjacent coastal area in which they were tagged. This indicates, at least for South Carolina waters, that management measures can probably be confined to individual estuarine systems rather than large coastal regions.

ACKNOWLEDGMENTS

Dr. G. Robert Lunz, Director of the Bears Blu Laboratories, gave advice during the study ar reviewed the manuscript. Thanks are also extend to W. A. Van Engel and F. J. Wojcik, Virginia Fis eries Laboratory, for review of manuscript. Sta members of the Bears Bluff Laboratories and t Biological Laboratory, Bureau of Commercial Fis eries, Beaufort, North Carolina, helped to tag crab

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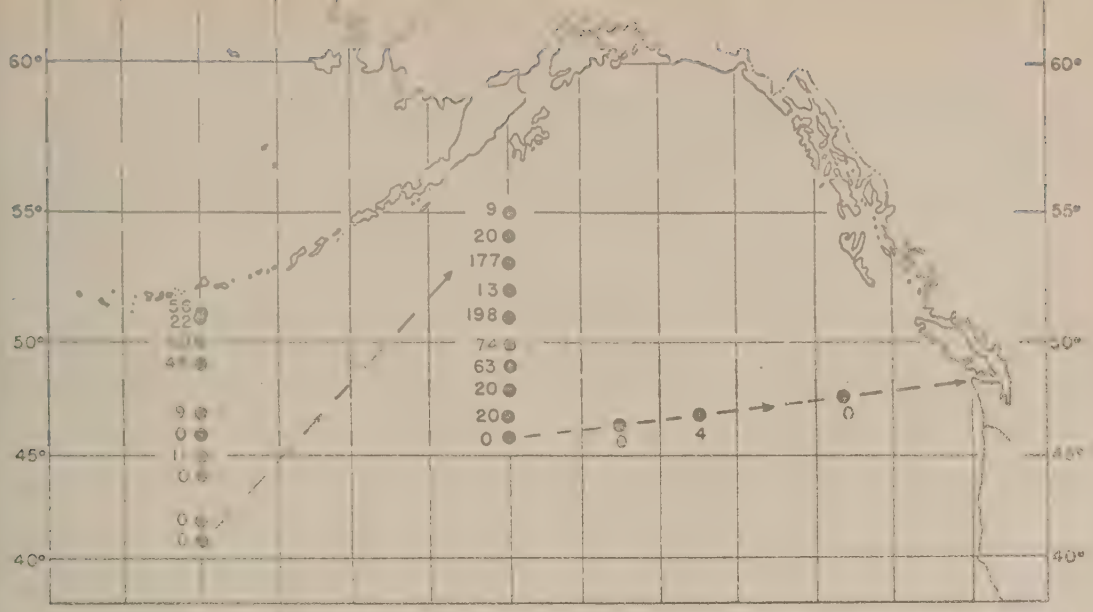

Salmon Catches made by the U. S. Bureau of Commercial Fisheries expedition aboard the Bertha Ann from uary to mid-April, 1962, are indicated at the fishing stations where they were made

Mid-Winter Gillnetting in Mid-Ocean

By ROBERT FRENCH and KENNETH MOSHER

A winter gill-netting cruise just mpleted by the U. S. Bureau of mmercial Fisheries charter vessel *rtha Ann* marks a milepost in sci- ific research into the ocean distri- tion of salmon in the North Pacific. r the first time, immature salmon re taken at sea during the winter son.

From late January until mid-April research vessel, with Capt. Erling obsen as master, was employed to dy the winter distribution of sal- n in the North Pacific Ocean. The ise was part of the Bureau's con- uing high seas research program nducted under the auspices of the erican section of the International rth Pacific Fisheries Commission, d marked the first efforts at win- time operations in high seas areas. entific personnel on the cruise were mes Mason, biologist-in-charge, and lix Favorite, oceanographer. Assis- nts were Robert Carlson, Alan Ha- wood, and Robert Preston.

The purpose of the fishing cruise s to study the distribution and rela- e abundance of salmon during win- ter periods and to determine how the food supplies, water temperature and other features of the ocean influence the location of the fish. Fish samples were obtained for laboratory analysis to determine the continent and river system of origin. Although much is known of the salmons' distribution in spring and summer months, nothing is known of their whereabouts in other seasons. It is vitally important to know where oceanic salmon are during all seasons in order to determine the vulnerability of various stocks to the Japanese high seas fishery and to estimate their abundance for management of the American inshore fisheries.

● Conventional nylon gill nets were used to catch these salmon. Each night when weather permitted approximately two miles of gill nets of different mesh were fished. On this trip six different sizes were used—2, 2½, 3¼, 3⅞, 4½, and 5¼-inch nets.

For the 2" mesh netting 2-ply twine, which fishermen generally called "No. 23 nylon" was used. The 2½" and 3¼" web was made of 3-ply or "No. 33 nylon." For the 3⅞" and 4½" web the twine was 4-ply or "No. 43 nylon." The 5¼" web was of 5-ply "No. 53 nylon."

The gillnets were all four fathoms deep, the number of meshes of course varying with the size. Cork and lead lines were of nylon, with a 12" selvage at the bottom to prevent rolling in the sea.

During the fishing process the gill nets were set in the evening between the hours of 6:00 and 8:00 p.m. The gear was allowed to soak all night, then was retrieved in the morning commencing at about 6:00 a.m. The net hauling process, during which the salmon were recorded by species, by mesh size in which they were caught, and by direction in the net, takes approximately 3 hours.

Oceanographic casts and plankton hauls were made at 30 to 60-mile intervals throughout the cruise. Water samples were analyzed aboard the vessel by means of a salinometer. During the trip 3,600 drift bottles were released, which upon recovery will pro-

acific Fisherman Vol. 60, no. 7 June 1962 p. 16-18.

rtha Ann is a stalwart sort, and she needed to be in the Gulf of Alaska and along the Aleutians in mid-winter. e is a former Army FS vessel 176' long and 550 tons. Photo by Mildred Ericson.

e information on ocean currents.

Fishing was done on two main sta- n tracks with three stations added the homeward journey, as indicated the accompanying sketch. Red sal- n dominated in the catches and re distributed among the different s as shown. The catch by species s 801 Red, 181 Chum, 5 Pink, 19 ver, and 1 King salmon, a total 1,011 salmon. Six Steelhead were en. Most of the Chums were taken the eastern leg of the cruise, with ly 19 being taken on the western . All salmon speciment were frozen oard the vessel and returned to Se- le for analysis.

Of special interest was the fact that mon, both maturing and immature, re caught near the Aleutian chain this season. It has been previously orized that salmon would be found more southern waters during win- months. As a matter of fact, in e western area along 175°W. longi- de no salmon were taken in the three uthernmost stations south of 45°N. itude at 44°, 42°, or 41°N. latitude.

Most of the Red salmon taken on is cruise were found along 155°W. ngitude, indicating a concentration fish in this area of the Gulf of laska. Any information we can ob- in as to the mainland localities of igin of these fish will be of value forecasting runs to the various eas. The age composition for each the catches along this line has en determined as an indication of the possible mainland origin of the fish.

● Red salmon generally live from 3 to 7 years from the time they were spawned, with most of them being approximately 4, 5 or 6 years old when they begin their spawning migration. The young fish normally spend 2, 3 or 4 winters in their fresh water habitat before migrating to the sea, where they live for 2 or 3 additional winters before maturing. Some occasionally mature after only one winter, the "jacks"; and a very few stay at sea as long as 4 winters.

In the four northern samples from 55° to 52°N. latitude south of Kodiak Island the fish were predominantly 5 and 6 years old. About 86% of the Red salmon in the large catch at 53° N. were of these two ages. Sixty-seven percent of this sample had been at sea for three winters and would have matured this year. Many of the two-winter in-the-sea fish would also mature this season. Mainland localities where these age combinations are the most common are in Bristol Bay, Kodiak Island, and along the Alaska Peninsula and northern Gulf of Alaska to the Copper River.

In the samples from 51° to 47°N. latitude the fish were predominantly 4- and 5-year olds. In the large catch at 51°N. approximately 71% were of these two ages. In contrast to the large catch made just 2 degrees to the north, 66% of this sample had been at sea only 2 winters. While many of these would have matured this year, a substantial percentage undoubtedly would not mature until 1963. Small numbers of fish of only one winter at sea were found in these southern catches. These almost without exception would hold over at least 1 year and some of them perhaps 2 years before maturing. No 6-year-old fish were found south of 49°N. latitude. Most of the southern fish had lived in fresh water for three winters. Fish of these fresh water and ocean ages are found in Bristol Bay, at Kodiak Island, in the Nass River of British Columbia, and in some years in other areas with relatively small Red salmon runs.

Four-year old fish which spend two winters in fresh water comprise the bulk of the runs to the Fraser and Columbia Rivers. Good percentages of fish of this age group were encountered only in the two southernmost samples where fish were taken. Fishing was relatively poor at these locations. These results indicate that the Red salmon taken along 155°W. longitude were widely mixed by stream of origin and that concentrations of fish intended primarily for a specific mainland locality were not present at the time of this cruise. Most of them will probably go to Central Alaska or Bristol Bay.

Despite rough weather and adverse fishing conditions, the trip proved that wintertime research cruises were possible in the North Pacific Ocean and

that extremely valuable information can be gained. It is very possible that abundance indices of maturing salmon runs can be obtained in winter or early spring months.

EDITOR'S NOTE — While the authors of this significant article on mid-winter gillnetting in mid-ocean do not specifically emphasize the point, it is readily noted that the findings discussed in the next-to-the-last paragraph of the article tend to support the forecast of a small Sockeye run to the Fraser River in 1962. Salmon of this species with age pattern characteristic of the Fraser and the Columbia Rivers appeared only in the southernmost catches along 155° west longitude. Furthermore, the numbers of Sockeye taken at these stations were small.

CONTINENTAL ORIGIN OF RED SALMON AS DETERMINED FROM MORPHOLOGICAL CHARACTERS

by

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ABSTRACT

In a comparative study of the morphology of populations of red salmon (*Oncorhynchus nerka*) from Asia and North America started in 1955, reference samples were collected from all principal red salmon streams and fisheries of North America. Samples of red salmon of Asian origin were obtained from the Okhotsk Sea near the southwest coast of the Kamchatka Peninsula. Samples to be identified as native to Asia or North America were obtained from the North Pacific Ocean and Bering Sea. Seven meristic characters showed promise as useful indices of continental origin and were unaffected by intra-area sources of variation.

On the basis of supplementary biological evidence, we classified high-seas samples as being of western Alaska or southwestern Kamchatka origin, using the discriminant function analysis. Western Alaska red salmon dominated most samples taken in 1956 eastward from longitude 175°E.; southwestern Kamchatka red salmon dominated westward from that longitude. Appreciable quantities of western Alaska red salmon occurred as far west as longitude 170°E. and appreciable quantities of southwestern Kamchatka red salmon appeared to occur as far east as 175°W., south of the Aleutian Islands. In May and June of 1957, western Alaskan red salmon dominated east of 180° and southwestern Kamchatka red salmon dominated as far eastward as longitude 175°E.

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INTRODUCTION

TREATY PROBLEMS AND TERMS OF REFERENCE

The International Convention for the High Seas Fisheries of the North Pacific Ocean was signed in Tokyo, Japan, on May 9, 1952, by representatives of Canada, Japan, and the United States of America. The negotiation of this treaty was in the interest of perpetuating valuable fishery resources in the North Pacific Ocean and Bering Sea. The circumstances culminating in the negotiation of this Convention have been summarized by Herrington (1952). This Convention introduced a new principle in international conservation practice on the high seas. Under it, special treatment is accorded to fisheries already fully utilized and fully conserved, each signator agreeing to abstain from exploitation of specified fish stocks that were already exploited to the maximum by one or both parties, provided the latter were carrying out programs for the conservation of stocks and agreed to continue such programs (U.S. Department of State, 1952).

By stipulation in the Annex to the Convention, Japan agreed to abstain from fishing for the five principal species of salmon (*Oncorhynchus gorbuscha*, *O. keta*, *O. kisutch*, *O. nerka*, and *O. tshawytscha*) in the North Pacific Ocean east of a provisional line following the meridian passing through the western extremity of Atka Island (Annex 1 (c), International Convention for the High Seas Fisheries of the North Pacific Ocean, 1952). In the Bering Sea, both Japan and Canada agreed to abstain from fishing those same species east of a line starting from Cape Prince of Wales on the west coast of Alaska, running westward to longitude 168°57′22″W.; thence due south to latitude 65°15′N.; thence along the great circle course which passes through latitude 51°N. and longitude 167°E., to its intersection with meridian 175°W.; then south along a provisional line which follows this meridian to the territorial-waters limit of Atka Island (Fig. 1).

The Protocol to the Convention further stipulates that the lines delineating abstention areas as defined by the Annex are conditional lines which shall continue in effect subject to confirmation or readjustment in accordance with results of studies to determine if there are areas in the ocean in which salmon originating in rivers of North America intermingle with salmon from the rivers of Asia.

Thus, the final terms of the Convention are dependent upon the identification and assignment of salmon taken on the high seas to their continents of origin. As one of several possible means by which this objective could be accomplished, the Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service, began a study of the morphology of salmon to determine the usefulness of meristic characters in determining the continental origin of fish taken on the high seas. The objective of this research was to determine the distribution on the high seas of red salmon (*Oncorhynchus nerka*) of both Asian and North American origin.[1]

BIOLOGICAL BASIS FOR STUDY

Robson and Richards (1936) have stated—

> The formation of groups having some degree of distinctness seems to be a universal property of living organisms, and the whole scheme of animate nature reveals itself as a hierarchy of groups beginning with simple aggregates of the status of the pure line, the clone, and the colony developing in distinctness and individuality through the local race to the species and higher categories.

The polytypic concept of species in fishes was first investigated by Heincke (1898) and reported in his classical work on the "local forms" of European herring. Subsequently, many fishery investigators have reported on subspecific divergence in meristic

[1] The International North Pacific Fisheries Commission, established in 1953 by the International Convention for the High Seas Fisheries of the North Pacific Ocean, coordinates the research of the member nations: Japan, Canada, and the United States. The resulting investigations provide the Commission data for use in carrying out its duties in connection with fishery conservation problems in the North Pacific Ocean.

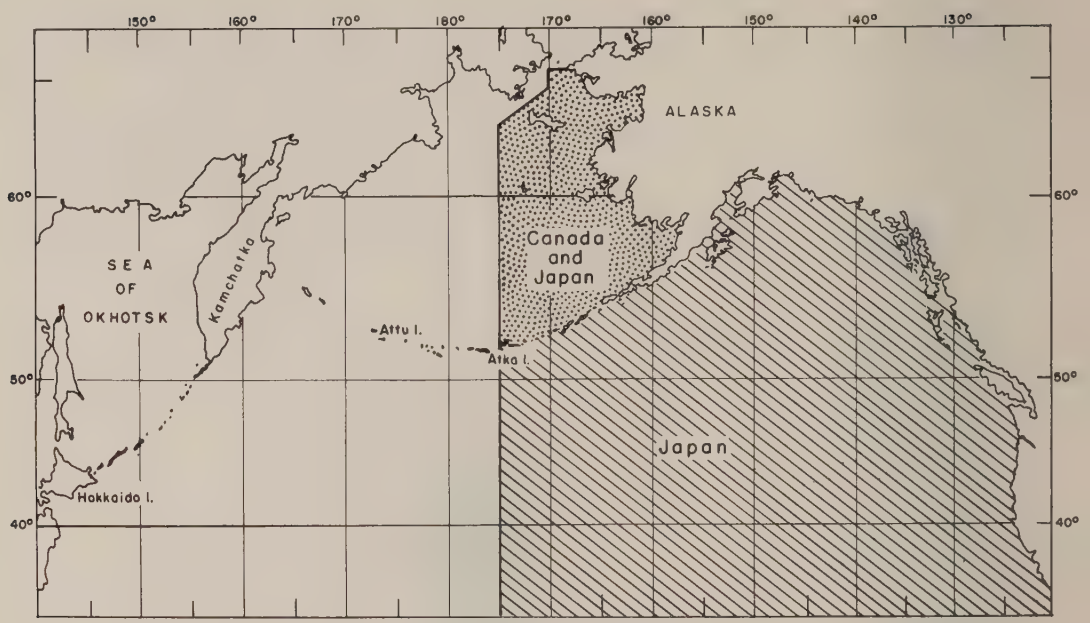

FIGURE 1. International North Pacific Fisheries Convention waters showing areas of Japanese and Canadian-Japanese abstention.

characters and the possible causes for these variations for many species of fish.

The maintenance of the identity of subspecific entities is dependent on geographic or reproductive isolation. Some unique restrictions to random interbreeding in the Pacific salmon present optimal circumstances for the development of ecological or geographic races.

Although more than one species of salmon spawn in many river systems, interbreeding of the five species of salmon appears to be minimal. Apparent crossbreeding of pink and red salmon was reported by Gibson (1929). Bonham and Seymour (1949) quoted hatchery attendants as frequently observing the crossmating of silver and king salmon on the spawning grounds of the Samish River, Washington. Experimental crossbreeding was accomplished in salmon by Gaylord and Marsh (1914) and Foerster (1930). The survival and perpetuation of hybrids is questionable, for Gaylord and Marsh observed them to be greatly inferior in vigor to the constituent species and expressed doubt that they could maintain themselves. Foerster had no knowledge on the natural occurrence of hybrids and questioned their fertility.

A further restriction to random interbreeding in the genus *Oncorhynchus* is the propensity of individuals to return to their natal streams to spawn. Although the home-stream theory has on occasion been questioned, salmon biologists have presented much e dence in its support. Results of these experime have been compiled and evaluated by Scheer (193 and Shapovalov (1940). The preponderance evidence certainly strengthens the case for homi and there appears little doubt that the Pacific salm of North America almost always return to spawn their natal streams.

In his discussion of the salmon resources of weste Kamchatka, Semko (1954) reports red salmon having the most pronounced homing tendency a pink salmon as displaying the greatest tendency stray. However, even in pink salmon 70 to 100 p cent were reported to return to their native strea

The case for homing in Hokkaido salmon appe to be not so clearly demonstrated; however, in course of evaluating a program of artificial propag tion of chum salmon, Sano (1951) obtained inform tion in support of the home-stream theory. Simi evidence for a homing tendency in pink salmon Hokkaido was obtained as a result of transplantati experiments (Sano and Kobayashi, 1953).

Differences in the timing of the red salmon runs the various streams of Kamchatka have been report by Taguchi (1957).

These restrictions to random interbreeding betwe populations are conducive to maintenance of

morphological identity of the various races of Pacific salmon and genotypic variations between races may be expected to occur. In addition to these variations, however, circumstantial and experimental evidence has shown that although heredity exerts a control in determination of meristic elements in fishes, factors in the physical environment, particularly during critical stages in embryonic and larval development, also influence the fixation of characters.

Association of temperature (or latitude) with the number of meristic elements in fishes has been investigated by many fishery workers. Jordan (1891) postulated an inverse relation between vertebral number and water temperature. Corroboration of this relationship has been documented by Schmidt for *Zoarces viviparus* (1917a, 1917b, 1920, 1921) and for *Lebistes reticulatus* (1919). Similiar observations for the Pacific herring, *Clupea pallasii* Cuvier, have been reported by Rounsefell and Dahlgren (1932), Tester (1938), and McHugh (1954a), and for the European herring, *Clupea harengus* Linn., by Runnström (1941).

The relationship of vertebral number to temperature has also been studied for flatfish (Rollefsen, 1939 ; Devold, 1942 ; Dannevig, 1950), cod (Schmidt, 1930 ; Dannevig, 1933), trout (Schmidt, 1921 ; Mottley, 1937), killifish (Gabriel, 1944), northern anchovy (McHugh, 1951), cyprinids (Weisel, 1955), and for *Lycodes pingelli*, *Ammodytes lancea*, *Gadus callarias*, and *Clupea harengus* (Jensen, 1944). The effect of salinity on meristic characters has been discussed by Heuts (1946, 1949) and the effects of light reported by Vladykov (1934), McHugh (1954b) and Lindsey (1958). Oxygen tension as an influencing factor was demonstrated by Tåning (1952) and Seymour (1956).

Studies on the effects of physical environmental factors on meristic characters in the family Salmonidae have not been extensive. Schmidt (1921) reared *Salmo trutta* at three different temperatures. He showed that the lowest number of vertebrae was produced at the intermediate temperature, the value rising both with higher and lower temperatures. Working with the sea trout, *Salmo trutta trutta*, Tåning (1952) found the vertebral number lowest at 6°C. While the counts increased both with lower as well as higher temperatures, the highest counts were obtained at 12°C. The number of fin rays in the dorsal, anal, and pectoral fins was highest at intermediate temperatures, decreasing at both higher and lower temperatures. Variations in vertebral and fin-ray numbers were not great under controlled constant temperatures. Tåning indicated that meristic characters determined in later embryonic life (i.e., number of fin rays) seem to be determined first and foremost by metabolism, whereas characters determined early (e.g., vertebral number) are to a greater extent controlled genetically. Mottley (1937) presented conflicting evidence. He observed that fish reared in the hatchery had vertebral counts significantly different from those of their own parents. Broods reared in parallel under similar conditions also differed in vertebral count.

Seymour's experiment (1956) with king salmon (*O. tshawytscha*) also showed that the lowest number of vertebrae occurred at intermediate temperatures, the vertebrae increasing in number with both higher and lower temperatures. This finding was essentially in agreement with the results of Tåning, who found that decreasing O_2 pressure led to an increase in the number of vertebrae in trout, whereas rising CO_2 pressure resulted in a decrease. A similar relation between O_2 tension and number of vertebrae was observed by Seymour in developing king salmon fry.

Thus, it has been demonstrated for many fishes including the salmon that ontogenetic development is affected by environment as well as by heredity, and morphological variation may be of phenotypic or genotypic character.

In North America, one or more of the five species of *Oncorhynchus* with which the Convention is concerned are indigenous to thousands of streams that flow into the Pacific Ocean, Bering Sea, and Arctic Ocean, from the Sacramento River northward as far as the Mackenzie River in the Canadian Arctic. Westward from the Alaska Peninsula they are distributed in the Aleutian Islands and the Komandorskii Islands. In Asia, the Pacific salmon are distributed from Korea and northern Japan northward and northeastward in streams tributary to the Sea of Okhotsk, North Pacific Ocean, Bering Sea, Chukchi Sea, and the Arctic Ocean. Because of this very extensive distribution of the genus, the geographic races of salmon are certainly subjected to different environments during embryonic and juvenile development. Then, with the combination of both genotypic and phenotypic effects, perceivable and measurable morphological differences may be expected to occur at the racial level in the species of the genus *Oncorhynchus*.

Table 1 shows the number of meristic characters for red salmon obtained from various sources in Canada, the Union of Soviet Socialist Republics, and the United States. It is readily seen that comparable data are not available from all sources, indicating very limited efforts in the past toward systematically uniform studies in the comparative morphology of these species.

Kawakami (1900) found significant differences in

TABLE 1. Counts of meristic characters for red salmon, from various sources.

Reference[1]	Branch-ioste-gals	Gill rakers	Anal-fin rays	Dorsal-fin rays	Scales above lateral line	Scales along lateral line	Scales below lateral line	Pyloric caeca	Ve br
Jordan and Evermann, 1896	13–15	32–40	14–16	11	20	133	20	75–95	64
Schultz, 1936		30–50	14–15		18–26	125–145	17–27		
Carl and Clemens, 1948		30–39	13–16			125–143		66–92	
Clemens and Wilby, 1949	11–15	30–39	13–17	11–16		125–139		66–92	
Berg, 1940	13–15	30–40	III–IV 13–15	III–V 9–10		130–142		75–95	64

[1] See Literature Cited.

several morphological characters between two races of chum salmon in Hokkaido. Subsequently, Kubo (1950) studied the correlation between stream-water temperature during a sensitive developmental period and the number of vertebrae, lateral-line scales, and other segmentally arranged structures in chum salmon from three tributaries to the Ishikari River, Hokkaido, Japan. The adults of the three populations were found to be significantly different in the number of segmentally arranged structures.

Pravdin (1929) studied the pink salmon of western Kamchatka. Although his work was primarily a detailed study in morphometric methodology he included some meristic data which he observed to differ from similar data published by Jordan and Evermann (1896) for Alaska pink salmon. Pravdin asked if the pink salmon of the eastern part of the Pacific Ocean were a local form. He mentioned the possibility of attributing the discrepancy to the exceeding difficulty in enumerating transverse rows of scales and pyloric caeca.

McGregor (1923) reported differences between Klamath River and Sacramento River king salmon in number of pyloric caeca, ova, gill rakers, and vertebrae that were of sufficient magnitude to distinguish individuals of the two races. In subsequent studies of Columbia River and California king salmon by Parker (1943) and Townsend (1944), the overlap in these characters was demonstrated to be so great as to make them of no practical value for identifying individuals of the various races.

Pritchard (1945) compared the average counts of gill rakers and pyloric caeca in samples of pink salmon taken from various streams in British Columbia. He found that in certain cases significant differences between areas was demonstrable while in others no variation seemed to exist.

These reports of meristic variation in salmon races are inadequate as a basis for evaluating the use of meristic characters as indices for racial separat The racial studies mentioned have been concer with differentiation of populations not widely se rated in space. With the exception of the curs comparison made by Pravdin, no attempts have b made to measure divergence in meristic parame between populations from widely separated ar within or between continents. Furthermore, in th earlier studies, characters were treated individu with statistical techniques which tested these vari for significance of differences in means betw populations. When characters that overlap are u to differentiate between populations of salmon, efficiency of differentiation may be increased simultaneous consideration of many characters. F thermore, it is not sufficient to know that the popu tions differ significantly with respect to any or al these characters. It is desirable to obtain measu of the magnitude of these differences and to utilize differences between combined meristic parameter classify individuals or groups of fish to their par groups. Mathematical statisticians have develo such techniques.

The generalized distance function, first proposed Mahanolobis (1936), is one of the best methods differentiating racial stocks and of describing th relation to one another. It was subsequently appl in an anthropometric survey by Mahanolobis, M jumdar, and Rao (1949), and described in mather tical terms by Rao (1952). In this method, differences between pairs of measurements from t or more sources are pooled to form an index of similarity called the generalized distance functi When samples of salmon of undetermined continer origin (viz., samples collected on the high seas) included in a function computed with continer reference areas, in effect the generalized dista function analysis becomes a means by which en samples (viz., all salmon of a given species taken a certain day at a specific place) can be classified. U of this method presumes the sample to be classified

a homogeneous group of individuals of common racial origin.

The discriminant function analysis (Fisher, 1936) is another method of classifying individuals from a mixed sample into their natal groups. In this method, multiple measurements from two reference populations are used to determine a criterion which best separates individuals of the two groups. Applying this criterion, individuals in samples, from a mixed population, are then classified into the alternative populations according to values of the same multiple measurements.

The purpose of this report is to apply the technique of discriminant function analysis to red salmon meristic data and assess the contribution of the results in determining the high-seas distribution of Asian and North American red salmon.

Two problems will be discussed in this report. The first problem concerns the selection of characters to be used as indices for racial separation; the intra-area variability of these characters; and the bias involved in sampling. The second problem considers the assumptions surrounding use of the discriminant function analysis; the selection of areas to be used and construction of the discriminant function; an empirical test of the constructed function; and applicability of the discriminant function in classifying red salmon taken on the high seas to continent of origin.

Supervision and coordination of the sampling program was the responsibility of Alvin E. Peterson, U.S. Bureau of Commercial Fisheries. At his request, the Japanese Fisheries Agency arranged for and collected samples from the Japanese high-seas mothership fishery and research vessels that operated in the North Pacific Ocean, Bering Sea, and Okhotsk Sea. The Fisheries Research Board of Canada provided samples from the streams and fisheries of British Columbia and from the high-seas waters of the Gulf of Alaska. Samples from the United States were obtained primarily by personnel of the Seattle Biological Laboratory, Bureau of Commercial Fisheries, with facilities and assistance provided by the Bureau's Alaska Regional Office. Samples from Wood River and Kvichak River were obtained through the cooperation of the Fisheries Research Institute of the University of Washington.

Reynold A. Fredin suggested use of the discriminant function analysis. Donald Worlund provided instruction and technical advice on this and other multivariate analytical techniques. He also programmed the sequence of multivariate analysis for the International Business Machine Computer-650 and together with Ernest Decorvet did all electronic computations.

George F. Slusser supervised the preparation, examination, and collection of meristic data. Members of his staff were Martin G. Beam, Robert Carlson, Donald E. Lewis, Roger E. Pearson, Carl G. Safsten, and Arthur Sullard. Kenneth H. Mosher provided the age readings.

The following persons kindly read our manuscript and provided useful suggestions and criticisms: Frederick Cleaver, Rea Duncan, James Mason, Ralph Silliman, and the staff of the Alaska Region of the Bureau of Commercial Fisheries; Dr. William F. Royce, Fisheries Research Institute, University of Washington; and Dr. Rosedith Sitgreaves, Teachers College, Columbia University.

PROBLEM I. SELECTION OF MORPHOLOGICAL CHARACTERS

A spawning population of red salmon returning to a particular stream is composed of both males and females. The number of years of lacustrine and marine existence is not common to the population, and age at maturity also varies. Many streams are known to contain several to many subpopulations which may migrate past the point of sampling at different times. Each of these categories within a stream population is a possible source of variation in morphological characters. The effects of any of these sources of variation will determine the grouping of data for inter-area comparisons (e.g., should the sexes be found to differ consistently in their distributions of meristic characters for inter-area comparisons, it will be necessary to consider them separately). For this reason, as an initial step to utilizing morphological characters as a means of identifying river races it was necessary to assess the effects of these internal sources of variation.

Several types of gear were used in collecting specimens for these studies; consequently, some selection for length may be anticipated. Should the characters here considered be related to fish length, inter-area comparisons must be confined to fish of comparable length. If the entire sample is to be used, then the alternative would be to discard from further consideration all characters closely associated with fish length.

METHODS AND AREAS OF SAMPLING

Sampling in North America

Red salmon were collected in North American

streams at several selected sites having weirs or other research or management installations. At each of these sites an attempt was made to obtain samples during the height of the run. Such could not always be done since the height of the run can only be known in retrospect, and occasionally transportation problems made it impossible to obtain samples at the desired time and place. At some sites, sampling was repeated during the run to assess the intra-area variation in meristic characters attributable to differences in time.

TABLE 2. Red salmon used in the analyses, collected in 1955.

Locality	Date caught	Number in sample
Bristol Bay:		
Naknek weir	7/9	[1]25
Do	7/15	25
Attu Island	7/28–10/30	52
Kodiak Island:		
Karluk weir	7/16	50
Do	7/29	50
Do	8/24	50
Do	9/12	50
Red River	7/6	30
Do	8/24	30
Fraser River:		
Cultus Lake	10/17–20	56
Adams River	10/11	30
Do	10/15	30

NOTE. These samples were included in the preliminary analyses only. Inadequacy of sample size precludes the use of them and most other 1955 samples in the classificatory analyses.

TABLE 3. Red salmon used in the analyses, collected in 1956.

Locality	Date caught	Number in sample
Stream Samples:		
Bristol Bay:		
Naknek weir	7/6,8	191
Egegik weir	7/17	204
Ugashik weir	7/23	196
Kvichak River	7/13	199
Wood River	7/11	195
Kodiak Island:		
Karluk weir	6/22	200
Do	9/7	200
Red River	6/17,18	196
Anchorage:		
Fish Creek weir	7/26–30	162
Cottonwood Creek weir	8/1	30
Chignik Lagoon	7/16–8/9	96
Attu Island:		
Lake Cories	7/15–8/4	219
Lake Nicholas	8/18–9/2	
Gravel pit	7/16–9/1	
Kagalaska Island	7/17–8/5	2
Unalaska Island:		
Volcano Bay	7/11,16	1
Rivers Inlet:		
Owikeno Lake	October	
Columbia River	6/26,7/2	
Do	8/2,14	
Inshore-Fisheries Samples:		
Teller	7/17–19	
King Cove:		
Cape Lutke	6/26	
Copper River:		
Cordova	6/15,26	2
Yakutat	8/4	
Petersburg	7/13	
Do	7/13	1
Ketchikan	7/13,23	
Do	7/31	
Do	8/2	
Nass River	8/6	
Skeena River	10/26	1
Namu	April	
Rivers Inlet	7/16	1
Fraser River:		
Gulf of Georgia	8/7	2
High-Seas Samples:		
Okhotsk Sea:		
51°49′N., 154°06′E	6/21	1
52°08′N., 154°32′E	6/28	1
51°55′N., 154°13′E	7/6	1
51°22′N., 153°51′E	7/13	
Eastern Kamchatka:		
51°04′N., 163°08′E	7/25	1
51°40′N., 159°50′E	8/5	1
Bering Sea:		
55°59′N., 170°02′W	6/20	2
53°20′N., 178°14′E	6/26	1
Western Aleutians:		
49°35′N., 171°46′E	7/6	1
50°30′N., 176°07′E	5/25	
50°22′N., 176°04′E	5/28	
51°38′N., 173°38′E	6/5	
52°08′N., 170°52′E	6/5	
51°56′N., 172°30′E	6/15	
51°40′N., 170°58′E	6/15	1
51°00′N., 175°00′E	8/25	1
50°00′N., 175°00′E	6/16	
51°00′N., 180°	8/23	
Eastern Aleutians:		
50°59′N., 174°57′W	8/8	

TABLE 4. Red salmon used in the analyses, collected in 1957.

Locality	Date caught	Number in sample
Stream Samples:		
Nome:		
Salmon Lake	7/26	52
Kuskokwim River:		
Bethel	6/25	57
Do	6/27	40
Bristol Bay:		
Naknek weir	7/3	100
Do	7/5	100
Do	7/11	58
Do	7/12	100
Do	7/21	54
Do	7/25	100
Do	7/29	21
Egegik River	7/13	184
Ugashik River	7/19	186
Kvichak River	7/9	96
Do	7/10	92
Wood River	7/17	166
Kodiak Island:		
Karluk weir	6/20	95
Do	8/21	110
Do	9/9	95
Do	9/17	120
Red River	6/21	199
Chignik weir	7/25	43
Do	7/26	40
Do	7/27	61
Do	7/28	53
Attu Island:		
Lake Nicholas	7/4,8/5	58
Lake Cories	6/25–8/18	62
Lakes Cornica and Cories	7/2–8/3	19
Lake Cornica	8/9–18	28
Columbia River:		
Wenatchee River	8/12	60
Okanogan	8/14	49
Inshore-Fisheries Samples:		
King Cove:		
Shumagin traps	6/22	64
Do	7/11	55
Do	7/26	78
Copper River	6/24	79
Do	7/16	45
Do	8/1	75
Yakutat	8/1	200
Petersburg	7/11	210
Do	8/12	10
Ketchikan	7/15	11
Do	8/20	26
Do	8/14	41
Do	8/15	43
Do	8/16	49
Do	8/17	41
Nass River	7/4	97
Skeena River	7/19	103
Do	7/30	100
Rivers Inlet	8/12–13	89
Fraser River:		
Gulf of Georgia	8/1	73
Do	8/6	106
Do	no date	18
High-Seas Samples:		
Okhotsk Sea:		
52°08′N., 154°15′E	6/24	192
50°52′N., 153°28′E	7/4	195
51°16′N., 153°39′E	7/14	194
Eastern Kamchatka:		
52°33′N., 166°04′E	6/20	90
52°28′N., 161°42′E	6/30	97
High-Seas Samples—Continued:		
52°36′N., 161°21′E	7/10	114
51°39′N., 161°40′E	7/20	90
51°22′N., 160°15′E	7/22	107
51°13′N., 159°45′E	7/24	89
51°39′N., 162°16′E	7/1	53
51°28′N., 161°15′E	7/5	56
49°14′N., 158°11′E	7/10	60
49°02′N., 158°20′E	7/14	57
48°57′N., 158°30′E	7/15	46
Bering Sea:		
58°15′N., 179°10′E	6/27	58
58°10′N., 177°17′E	7/1	40
54°51′N., 170°24′E	7/6	38
57°02′N., 169°11′E	7/12	33
57°26′N., 167°27′E	7/13	30
58°12′N., 166°48′E	7/15	56
53°00′N., 175°00′E	6/20	58
53°00′N., 180°	6/22	47
56°00′N., 175°00′W	6/30	40
53°00′N., 175°00′E	8/11	57
53°00′N., 175°00′E	8/12	83
56°00′N., 175°00′E	8/14	40
53°00′N., 175°00′E	8/17	83
53°00′N., 175°00′E	8/18	60
53°00′N., 175°00′W	6/8	51
53°01′N., 175°03′W	6/9	53
53°00′N., 175°00′W	6/10	43
56°00′N., 175°00′W	6/15	193
56°00′N., 173°00′W	6/17	148
56°00′N., 170°00′W	6/18	86
56°52′N., 170°00′W	6/19	64
56°00′N., 168°00′W	6/21	61
55°00′N., 168°00′W	6/22	85
Western Aleutians:		
51°40′N., 167°27′E	6/29	42
51°15′N., 169°02′E	5/21	38
52°31′N., 168°27′E	6/25	43
51°28′N., 169°55′E	5/27	39
49°02′N., 167°25′E	5/31	63
48°08′N., 167°40′E	5/21	58
50°00′N., 175°00′E	6/10	40
50°00′N., 175°00′E	6/11	57
50°00′N., 175°00′E	6/12	54
51°00′N., 176°00′W	7/8	42
50°00′N., 175°00′E	8/8	39
51°30′N., 175°00′E	8/19	144
50°00′N., 175°00′E	8/20	85
51°30′N., 175°00′E	8/23	112
51°30′N., 175°03′W	8/6	45
50°59′N., 175°10′W	8/7	102
49°59′N., 175°00′W	8/8	76
50°00′N., 175°01′W	8/9	111
50°00′N., 175°01′W	8/20	46
50°00′N., 175°01′W	8/21	70
50°59′N., 175°01′W	8/22	106
51°31′N., 175°02′W	8/23	49
Eastern Aleutians:		
53°00′N., 165°00′W	7/24	100
53°00′N., 165°00′W	7,30,31	46
Gulf of Alaska:		
54°00′N., 160°00′W	7/15	51
52°00′N., 160°00′W	7/17	106

The areas and dates of sampling and the numbers of red salmon collected in 1955, 1956, and 1957 are given in Tables 2, 3, and 4. The locations of the sampling sites listed in Tables 3 and 4 are shown in Figures 2 and 3.

In 1956 and 1957 samples were obtained from streams considered major producers of red sa Curves illustrating escapement to several str with date or dates of sampling, are shown in App Figures A–1 to A–4, page 53.

To supplement the stream samples that rep the intra-continental references, samples were ob

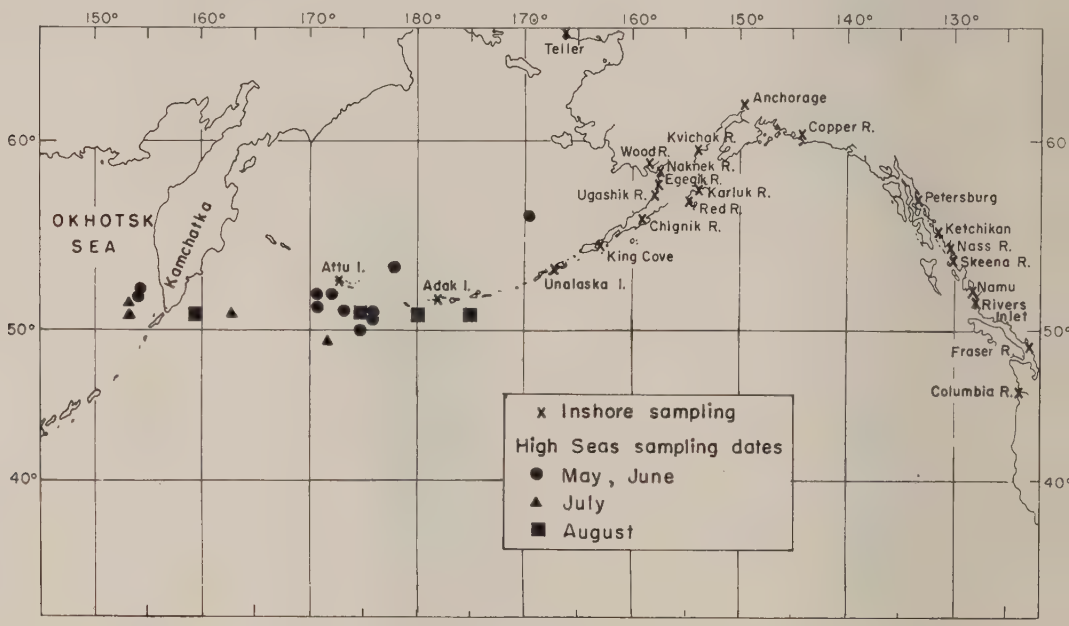

FIGURE 2. Collection locations of red salmon samples, 1956.

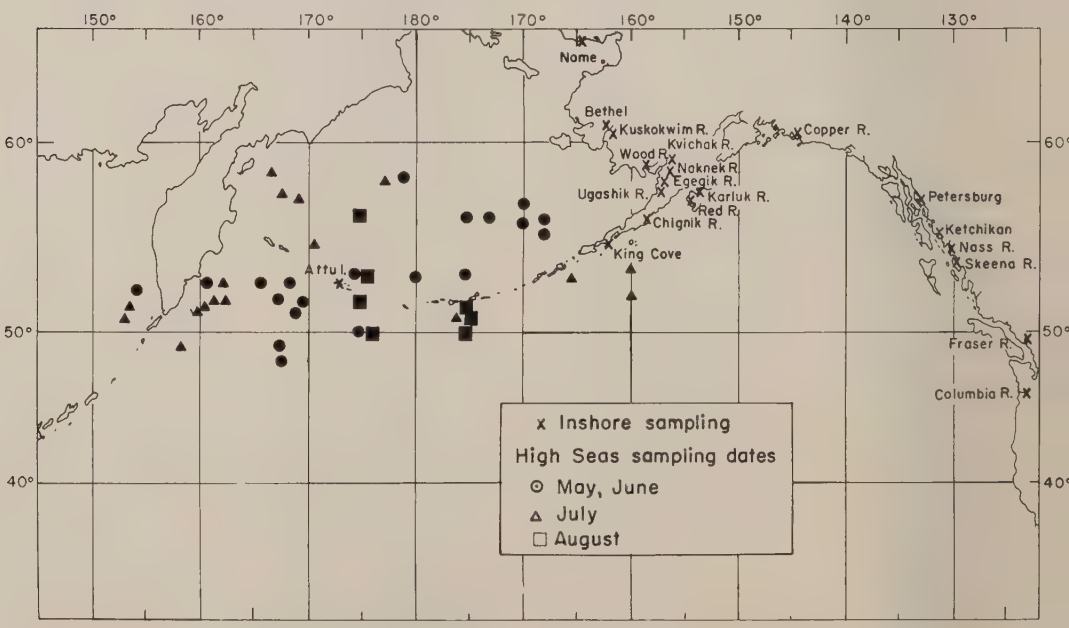

FIGURE 3. Collection locations of red salmon samples, 1957.

ring the fishing season from several estuarine fisheries North America.

The catch of red salmon for the three regions of aska for the years 1941 through 1957 is given in ble 5. Catches of red salmon in western Alaska, the average, constitute more than 60 percent of the tal red salmon catch of Alaska. The five principal er systems of Bristol Bay provided the bulk of this catch.

The catch of red salmon for British Columbia, Canada, for the years 1952 through 1957 is given in Table 6. The total landings for the 6 years show that the Fraser River contributed about 60 percent of the red salmon landings in British Columbia.

In 1955, samples from Canada were obtained only

TABLE 5. Landings of red salmon in Alaska, by regions, 1941–57.
[From Fishery Statistics of the United States (U.S. Fish and Wildlife Service, 1945–59)]

	Southeastern		Central		Western		
Year	Number of fish	Percent of annual landings	Number of fish	Percent of annual landings	Number of fish	Percent of annual landings	Total fish
1941	1,674,412	11	5,402,962	35	8,295,990	54	15,373,364
1942	1,566,489	12	4,990,776	39	6,355,029	49	12,912,294
1943	1,123,759	4	7,862,238	30	17,355,763	66	26,341,760
1944	1,722,276	8	6,056,829	30	12,389,101	61	20,168,206
1945	1,683,289	11	5,773,640	38	7,639,005	51	15,095,934
1946	888,241	6	4,604,245	32	8,981,988	62	14,474,474
1947	746,170	3	6,089,695	24	19,014,413	74	25,850,278
1948	524,525	3	4,313,910	22	14,815,611	75	19,654,046
1949	489,799	4	4,814,683	41	6,517,000	55	11,821,482
1950	552,202	4	5,947,097	43	7,266,949	53	13,766,248
1951	819,621	8	4,136,001	43	4,697,196	49	9,652,818
1952	919,336	5	4,341,432	26	11,663,736	69	16,924,504
1953	1,376,450	12	3,763,018	32	6,653,652	56	11,793,120
1954	1,207,877	13	3,189,722	34	5,013,662	53	9,411,261
1955	681,245	8	2,675,172	31	5,148,250	61	8,504,667
1956	920,778	6	3,431,907	23	10,252,393	70	14,605,078
1957	1,031,213	10	2,071,417	21	6,630,743	68	9,733,373
Total	17,927,682	7	79,464,744	31	158,690,481	62	256,082,907

TABLE 6. Commercial catch of red salmon in Canada and in Sockeye Salmon Fisheries Convention waters, 1952–57.
[Data from International North Pacific Fisheries Commission, 1952–1957]

	British Columbia						
	Northern[1]		Southern[2]		Fraser River[3]		
Year	Number of fish	Percent of annual landings	Number of fish	Percent of annual landings	Number of fish	Percent of annual landings	Total fish
1952	3,212,000	53.8	510,300	8.5	2,253,475	37.7	5,975,775
1953	3,108,900	39.1	823,100	10.3	4,027,137	50.6	7,959,137
1954	1,757,300	15.3	269,100	2.3	9,490,258	82.4	11,516,658
1955	1,456,900	37.9	271,500	7.1	2,113,710	55.0	3,842,110
1956	2,159,000	51.8	204,900	4.9	1,800,436	43.2	4,164,336
1957	985,600	20.9	700,300	14.8	3,039,365	64.3	4,725,265
Total	12,679,700	33.2	2,779,200	7.3	22,724,381	59.5	38,183,281

[1] Includes catch from British Columbia Statistical Districts 1 to 10 and 30.
[2] Includes catch from British Columbia Statistical Districts 11 to 16 and 22 to 27.
[3] Includes catch from British Columbia Statistical Districts 17 to 21, 28, and 29, as well as United States catch.

from the Fraser River. In 1956, the Nass River, Skeena River, Namu, Rivers Inlet, and the Fraser River were sampled. The 1957 samples were obtained from these same areas, excepting Namu.

Sampling in Asia

The principal red salmon streams in Asia are those of the Kamchatka Peninsula, and the best samples for our purposes would have come from those streams. Since such samples were not available, red salmon were obtained from Japanese mothership fisheries operating in the Okhotsk Sea off the southwestern coast of Kamchatka. Because these were mature fish (from evidence of age and gonad development) taken in late June and during July near the Kamchatka coast, it was assumed that they were red salmon of Asian origin. These samples were obtained at weekly or 10-day intervals. Most samples collected for our purpose were caught in gillnets with mesh of $4^{8}/_{10}$ inches stretched measure.[1]

Although the specific streams to which these red salmon would have returned cannot be established, evidence from tagging experiments (Sato, 1939) has shown red salmon from this area to be from streams of southwestern Kamchatka. Semko (1954) and Taguchi (1957) have reported that the southwestern Kamchatka red salmon district is by far the most productive of those surrounding the Okhotsk Sea.

The importance of this Okhotsk Sea collection in relation to the other Kamchatka red salmon populations is indicated in Table 7, the data for which were taken from catch statistics published by the International North Pacific Fisheries Commission (1959). On the average, the west coast of Kamchatka contributed about 89 percent of the total catch of Kamchatka red salmon. Thus, it seems reasonable to assume that our samples are mainly composed of western Kamchatka fish, and by virtue of the great contribution of this area to the total Kamchatka landing, these samples reflect the characteristics of the major populations of Kamchatka red salmon.

Sampling on the High Seas

Samples from gillnet catches on the high seas were obtained from the Japanese high-seas fishery, and from Japanese, Canadian, and United States research vessels. Each of these research vessels used a standard set of gillnets with mesh sizes of $2^{1}/_{2}$ inches, $3^{1}/_{4}$ inches, $4^{1}/_{2}$ inches, and $5^{1}/_{4}$ inches stretched measure. Specimens from the Japanese fishery were taken in $4^{8}/_{10}$-inch mesh.

[1] Distance between opposite knots.

TABLE 7. Catch of red salmon in U.S.S.R. fisheries for districts of Kamchatka, 1949–58. [In thousand metric tons; data from International North Pacific Fisheries Commission, 19

Year	West coast		East coast		
	Total catch	Percent of annual run	Total catch	Percent of annual run	Total catch
1949	8.3	94.3	0.5	5.7	8
1950	8.2	88.2	1.1	11.8	9
1951	7.0	91.0	0.7	9.0	7
1952	8.9	96.8	0.3	3.2	9
1953	5.0	98.1	0.1	1.9	5
1954	3.6	90.0	0.4	10.0	4
1955	2.4	77.5	0.7	22.5	3
1956	4.4	77.2	1.3	22.8	5
1957	2.9	82.9	0.6	17.1	3
1958	0.6	60.0	0.4	40.0	1
Total	51.3	89.4	6.1	10.6	57

Most high-seas samples in 1956 were taken in waters between longitudes 175°W. and 170°E., and latitudes 50°N. and 56°N. The number of samples was very limited, with most samples collected south of the Aleutian Islands.

High-seas sampling was considerably more extensive in 1957 than in 1956, with collections from waters bounded by longitudes 170°W. and 160°E. and by latitudes 50°N. and 59°N. In both years, samples were lacking from the Gulf of Alaska for use in our analyses.

All samples used in these studies were identified by time and place of collection and frozen for transshipment to the Bureau of Commercial Fisheries Biological Laboratory at Seattle, Washington.

The results of our sampling red salmon in 195[illegible] 1956, and 1957, may be summarized as follows:

Sampling in the North American continent was sufficiently extensive so as to include all major fishery and escapement areas. Included in these samples are specimens collected in all known major red salmon streams in North America. Some streams were sampled more than once during a single season. Samples to supplement those taken in streams were obtained from several major estuarine and inshore fisheries.

Specimens were obtained from the Japanese mothership fishery operating in the Okhotsk Sea in lieu of samples from Kamchatka streams. Although these samples cannot be identified with specific streams

Kamchatka there is good evidence that they were sh of Asian origin and probably individuals of pop- lations native to streams of southwestern Kam- hatka.

Extensive coverage was given the high seas of the North Pacific Ocean and Bering Sea by Japanese ommercial and research vessels and Canadian and United States research vessels. Sampling effort in he Gulf of Alaska, however, was not so extensive. Only two samples collected from this area in 1957 were included in our analysis.

DATA COLLECTION

Measurements and counts were made from struc- ures on the left side of the fish except when abnormal r mutilated. When necessary, the comparable struc- ure on the right side was substituted if no evidence of ilateral asymmetry was indicated; otherwise, the articular items were not recorded. Only specimens for which data on all characters were obtainable were included in the classificatory analysis.

Ten morphological characters were initially selected on the merits of their promise in separating various populations of red salmon within and between continents. Photographic copies of the radiographed characters are shown in Figure 4. The 10 characters and the methods of enumerating them are as follows:

1. *Number of scales along lateral line.*—Was obtained directly from each specimen by one person. This count included scales along the lateral line excluding the most anterior scale. Posteriorly, the count terminated at the posterior margin of the hypural plate, which was identified by an incision carefully made near the crease, which appears when the caudal fin is flexed. When more than half the scale or scale pocket remained anterior to the cut, it was included in the count. Frequently specimens from the high seas are denuded of scales, in which instances the scale

FIGURE 4. Photographic copies of radiographed meristic characters.

pockets were counted.

2. *Number of scales below lateral line.*—Was obtained by counting dorsally and anteriorly from the second scale anterior to the junction of the pelvic fin with the accessory appendage, to and excluding the lateral-line scale.

3. *Number of vertebrae.*—Was counted from radiographs, beginning with the atlas and terminating posteriorly with the urostyle. Occasionally, fusion of vertebrae (or duplicated vertebral processes) was encountered (in about 3 percent of specimens); fish with abnormal vertebrae were not included in these analyses.

4. *Position of first haemal arch.*—Was the numerical position of that vertebra in the vertebral column. Before the radiographing, with the aid of a probe, this structure was marked with a lead wire, which was readily identified on the radiograph.

5. *Number of ventral gill rakers.*—Included all rakers on the ventral arm of the first, left gill arch, including the raker in the bend of the arch. Branched rakers having a common base were counted as one and all rudimentary rakers were included. Occasionally, technical difficulties or the nature of a particular gill arch caused disagreement between readers in positively identifying rudimentary rakers at the anterior end of the ventral limb. Re-radiographing the particular gill arch usually resolved these difficulties, but where any doubt existed the structures were stained[1] and counted.

6. *Number of gill rakers.*—Included all rakers on the first, left gill arch. Criterion for enumeration was identical with that for character 5.

7. *Number of branchiostegal rays.*—Was obtained from radiographs of the branchiostegal. Disagreements in reading were resolved by enumerating the rays after staining.

8. *Number of pectoral-fin rays.*—Included all fin rays in the left pectoral fin as enumerated from radiographs.

9. *Number of elements in dorsal fin.*—All elements in this fin were enumerated, including the rudimentary rays which would normally be lost if fins were dissected for the counts. Occasionally, both in the dorsal and anal fins a small bone is present anterior to the first obvious rudimentary ray. Its existence has been substantiated by staining many fins where it was seen to occur in radiographs. If this bone was round with no indication of elongation as in other rudimentary rays, it was not included in the count.

10. *Number of elements in anal fin.*—Criteria and method of counting were identical with those for character 9.

Supplementary data pertinent to subsequent analyses were also obtained. These include the length of each specimen from the middle of the eye to the posterior margin of the hypural plate, body weights, and an age reading obtained from a scale.

Ages were determined by scale examination. Age designations are those of Gilbert and Rich (1927). The principal numeral is the total age and the subscript the number of winters the fish spent in fresh water (e.g., 5_3).

STATISTICAL PROCEDURES

Data were recorded on ozalid paper to simplify duplication of records when requested from cooperating and allied projects. These data were then transferred to punch cards. Analysis from this point was accomplished almost entirely by use of International Business Machine (IBM) equipment. Computations were done on an IBM 650 electronic computer.

The following preliminary statistical analyses were made:

Analysis of variance.—It was used to test the significance of differences among means of two or more groups, such as sexes, different year classes, et cetera. Since these tests assume common variance, the variance-ratio test and Bartlett's test were used to verify the assumption:

Variance-ratio test: In two samples the ratio of the larger mean square over the smaller was used to test the hypothesis that the two population variances were equal (Snedecor, 1956). Tabled percentiles for the F- distribution with appropriate degrees of freedom are used to determine the significance of an observed ratio. When the hypothesis is true, the probability of obtaining a value larger than the observed is twice the probability that the corresponding F-statistic will exceed the observed value (Pearson and Hartley 1956).

Bartlett's test: It tests the hypothesis that the variances of k-normally distributed populations are equal. The sampling distribution of the test statistic M is approximately X^2 with $(k-1)$ degrees of freedom where

[1] Stained by using a modified method of Hollister (1934).

$$M=(N-k)\log_e s_p^2-\sum_{i=1}^{k}(n-1)\log_e s_i^2$$

he expression s^2_p is the pooled variance, while s^2_i e the individual variances (Snedecor, 1956).

Combination of probability test.—When several tests the same hypothesis were made (for example, differ- ce between sexes with respect to a given character r all areas), we accepted or rejected at some level in dividual tests with no information on the significance f the number of rejections for the combined series. isher (1944) has shown that a statistic $C=-2\sum_{i=1}^{k}\log_e P_i$ as a X^2 distribution with $2n$ degrees of freedom and is the probability level for each of k tests.

Test for significance of correlation of bivariates.—To etermine the possible bias in sampling that might e introduced by gear selection, the correlation of all haracters to length was assessed. In a manner an- logous to the combination of probability tests for eans, correlation coefficients (r) of all samples were ooled by the technique of Z-transformation (Pearson nd Hartley, 1956: p. 31) and the significance of the ooled correlation co-efficient was determined.

ANALYSES FOR SELECTION OF CHARACTERS AND INTRA-AREA VARIATION

Results of past tagging experiments (Gilbert and ich, 1925) present some direct evidence that indi- ates the red salmon taken in estuarine fisheries may e an heterogeneous group of individuals migrating various streams. Although the mature fish in such roups are probably native to the adjacent continent, ithout supplementary evidence it is hardly appro- riate to assume that a sample of estuarine or inshore- ught red salmon are of common origin or from reams near their locality of capture. Such being the se, the results of tests designed to isolate effects of ithin-population sources of variation (e.g., sex, age, cetera) may be expected to be confounded by the fects of actual population differences. For this ason no detailed examination of internal variation Okhotsk Sea samples was attempted and only those mples obtained within North American streams ere analyzed in detail to assess the effects of intra- ea sources of variation.

Initially, the various components of the entire sample btained from each stream were assumed to be homo- eneous with respect to ten meristic characters. The lidity of this assumption was subsequently tested by ssessing the effects of possible intra-area sources of ariation such as sex, fresh-water age, ocean age, brood year, and time of sampling. Detailed tabulations of the results are presented in Appendix Tables B-1 to B-60). Only summary tables are included in the text.

Morphological data from samples obtained within streams during the 1955, 1956, and 1957 sampling seasons were sorted by area, date, age group, and sex. When so subdivided, observations in some categories were few, particularly in tests to determine sexual dimorphism and tests to determine the variation due to differences in time of sampling. Although we recognized the desirability of working with a minimum of 30 fish in each category, in the interest of retaining as many data as can be considered reasonable, 14 observations per class were arbitrarily considered the minimum. The effect of including samples of this size may be evaluated on the basis of the consistency of the results. Disagreement (of varying magnitudes) has been demonstrated to occur between scale analysts reading the same scale. Evaluation of these errors is not within the scope of this paper. We have, therefore, assumed all age readings to be accurate but acknowledge this to be a possible source of error.

Tests for Sexual Dimorphism

For the genus *Oncorhynchus*, differences between sexes in external morphology, particularly with approaching sexual maturity, have been described by many investigators. To test whether sexual dimorphism occurs also in the ten meristic characters considered here, stream samples collected in 1956 and 1957 were utilized.

The significance of differences between mean counts in males and females for each of ten meristic characters in all 16 of the 1956 stream samples and in 17 of the 1957 samples was tested to determine if sexual dimorphism existed in these characters (Table 8).

Considering all samples for each individual character, the combination of probability tests failed to show any evidence of sexual dimorphism in the 1956 collections. The combination of probability test for scales below the lateral line was significant at the 5-percent level in the 1957 collections. Examination of the variances for these tests reveals no apparent discrepancy in variances which may have caused the significant differences in the means for this character.

For the meristic characters tested, these results indicate a significant difference between sexes only in the number of scales below the lateral line.

TABLE 8. Analysis of variance for sexual dimorphism and tests for common variance, in red salmon collected in 1956 and 1957.
[Dash (—) indicates nonsignificant value]

Year and area	Date	Age group	Significance level for — Scales along lateral line: Means	Scales along lateral line: Variance	Scales below lateral line: Means	Scales below lateral line: Variance	Total vertebrae: Means	Total vertebrae: Variance	First haemal arch: Means	First haemal arch: Variance	Ventral gill rakers: Means	Ventral gill rakers: Variance	Total gill rakers: Means	Total gill rakers: Variance	Branchiostegal rays: Means	Branchiostegal rays: Variance	Pectoral-fin rays: Means	Pectoral-fin rays: Variance	Dorsal-fin elements: Means	Dorsal-fin elements: Variance	Anal-fin elements: Means	Anal-fin elements: Variance
1956 :																						
Columbia River :																						
Bonneville	7/2	4_2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.05	0.05	—	—	—	—
McNary	7/12	4_2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Kagalaska Island	7/24	6_3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Do	7/31	6_3	—	—	—	—	—	—	—	—	0.05	—	—	—	—	—	—	—	—	—	—	0.05
Kodiak Island :																						
Karluk weir	9/7	6_4	—	—	—	—	—	—	—	0.05	—	—	—	—	—	—	0.05	—	—	—	—	—
Do	6/22	6_4	—	—	—	—	—	0.05	—	—	—	—	—	—	—	0.05	—	—	—	—	—	—
Do	6/22	7_4	—	—	—	—	—	—	—	0.05	—	—	—	—	—	—	—	—	—	—	0.05	—
Bristol Bay :																						
Naknek weir	7/8	5_2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Do	7/8	6_3	—	—	—	—	—	0.05	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Egegik weir	7/17	5_3	—	—	—	0.05	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ugashik weir	7/23	4_2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.05
Do	7/23	5_3	—	—	—	—	—	—	—	—	—	—	—	—	—	0.05	—	—	—	—	0.05	—
Kvichak River	7/13	4_2	—	—	—	0.05	—	—	—	0.05	—	—	—	—	—	—	—	—	0.05	—	—	—
Do	7/13	5_3	—	—	—	—	—	—	—	—	—	—	—	—	—	0.05	—	—	—	—	—	—
Wood River	7/11	4_2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cook Inlet :																						
Fish Creek weir	7/25	4_2	0.05	—	—	—	—	0.05	—	—	—	—	—	—	0.05	—	—	—	—	—	—	—
Combination of probability test, 1956			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1957 :																						
Columbia River :																						
Tumwater	8/12	4_2	—	—	—	0.05	—	—	—	—	0.05	—	—	—	0.05	—				—	—	—
Kodiak Island :																						
Karluk weir	9/17	5_3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Red River	6/21	5_2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.05	—	—	—	0.05
Do	6/21	5_3	—	—	—	—	—	0.05	—	0.05	—	—	—	—	—	—	—	—	—	—	—	—
Do	6/21	6_3	—	—	—	—	—	—	—	—	—	—	—	—	0.05	—	—	—	0.05	—	—	—
Bristol Bay :																						
Naknek weir	7/3	6_3	—	—	0.05	—	—	—	0.01	—	—	0.05	—	—	—	0.05	—	—	—	—	—	—
Do	7/5	5_2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Do	7/5	6_3	—	0.05	—	—	0.05	0.05	—	—	—	—	—	—	—	—	—	—	0.05	—	—	—
Do	7/11	6_3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.05
Do	7/12	6_3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Do	7/21	6_3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.05	—	—
Do	7/25	6_3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.05
Egegik weir	7/13	6_3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ugashik weir	7/19	5_2	—	—	0.05	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Kvichak River	7/9	5_2	0.05	—	—	—	—	0.05	—	—	—	—	—	0.05	—	—	—	—	—	—	—	—
Do	7/10	5_2	—	—	—	—	—	—	—	—	—	—	—	—	—	0.05	—	—	—	—	—	—
Wood River	7/17	5_2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Combination of probability test, 1957			—	—	0.05	—	—	—	—	—	—	—			—	—	—	—	—	—	—	—
Combination of probability test, 1956-57			—	—	0.05	—	—				—	—					—	—	—	—	—	—

Tests for Effects of Fresh-water Age

Red salmon hatched in the same year may spend from 1 to 5 winters in fresh water before migrating to sea. The number of elements in most of the ten meristic characters which are considered here is fixed during some stage of embryonic development and the length of residence in fresh water is not expected to contribute significantly to variation. To test this premise, significance of differences between mean counts was studied in nine samples of red salmon of the same year class and ocean age but of different fresh-water ages taken in North American streams. Combination of probability tests for individual characters show significant differences between the means for number of scales below the lateral line, number of branchiostegal rays, number of dorsal-fin elements, and number of anal-fin elements. With two exceptions, significant differences in means seemed not to be associated with discrepancies in the variances (Table 9).

Results of these tests indicate no effect of fresh-water age on the meristic characters included, except in number of scales below the lateral line, branchiostegal rays, and dorsal- and anal-fin elements.

Tests for Effects of Ocean Age

For the analyses of effects of ocean age on meristic counts, the data were arranged to test differences in means and variances of meristic characters between red salmon that spent 2 years and those that spent 3 years in the ocean. These fish had the same fresh-water age and brood year (Table 10).

The combination of probability tests for the differences between means show significant differences between red salmon that had spent 2 years in the ocean and those that had spent 3, in the number of scales below the lateral line, number of branchiostegal rays, and number of dorsal-fin elements. Significant differences between variances were sporadic and seemed not to be associated with significant differences between means.

TABLE 9. Analysis of variance for effects of fresh-water age and tests for common variance, in red salmon collected in 1955 to 1957.
[Dash (—) indicates nonsignificant value]

Area	Date	Age group	Significance level for — Scales along lateral line: Means	Scales along lateral line: Variance	Scales below lateral line: Means	Scales below lateral line: Variance	Total vertebrae: Means	Total vertebrae: Variance	First haemal arch: Means	First haemal arch: Variance	Ventral gill rakers: Means	Ventral gill rakers: Variance	Total gill rakers: Means	Total gill rakers: Variance	Branchiostegal rays: Means	Branchiostegal rays: Variance	Pectoral-fin rays: Means	Pectoral-fin rays: Variance	Dorsal-fin elements: Means	Dorsal-fin elements: Variance	Anal-fin elements: Means	Anal-fin elements: Variance
Kodiak Island:																						
Karluk weir	6/16, 29/55 6/22/56	6_3 7_4	—	—	—	—	—	0.05		—		—	—	—	—	—	—	—	—	—	—	—
Do	6/22/56 6/20/57	5_3 6_4	—	—		—			—	—	—		—	—	—	—		—	—	—		
Do	6/22/56 6/20/57	6_3 7_4	—	—	—	—	—	—	—	—	—	—	—	—	0.05	0.05		—				—
Do	9/7/56 8/21/57 9/9, 17/57	5_3 6_4	—	—	—		—	—	—	—	—	—	—	—	—	—	—					
Red River	6/17, 18/56 6/21/57	4_2 5_3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.01	—	0.01	
Bristol Bay:																						
Egegik weir	7/17/56 7/13/57	4_2 5_3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.01	0.05
Do	7/17/56 7/13/57	5_2 6_3	—	—	—	—	—	—	—	—	—	—	—	—	0.05	—	0.01	—	0.01	—	—	
Ugashik weir	7/23/56 7/19/57	4_2 5_3	—	—	0.01	—	—	—	—	—	—	—	—	0.05	—	—	—	—	0.01	—	—	—
Kvichak River	7/13/56 7/9, 10/57	4_2 5_3	—	—	0.01	—	0.05	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Combination of probability test			—	—	0.01	—	—	—	—	—	—	—	—	—	0.05	—	—	—	0.01	—	0.05	—

TABLE 10. Analysis of variance for effects of ocean age and tests for common variance, in red salmon collected in 1955 to 1957. [Dash (—) indicates nonsignificant value]

Area	Date	Age group	Significance level for — Scales along lateral line: Means	Scales along lateral line: Variance	Scales below lateral line: Means	Scales below lateral line: Variance	Total vertebrae: Means	Total vertebrae: Variance	First haemal arch: Means	First haemal arch: Variance	Ventral gill rakers: Means	Ventral gill rakers: Variance	Total gill rakers: Means	Total gill rakers: Variance	Branchiostegal rays: Means	Branchiostegal rays: Variance	Pectoral-fin rays: Means	Pectoral-fin rays: Variance	Dorsal-fin elements: Means	Dorsal-fin elements: Variance	Anal-fin elements: Means	Anal-fin elements: Variance
Kodiak Island:																						
Karluk weir	6/16,29/55	6_4	0.01	—	—	—	—	—	—	—	0.05	—	0.05	—	—	—	—	—	—	—	—	—
	6/22/56	7_4																				
Do	6/22/56	6_4	—	—	—	—	—	—	—	—	—	—	—	—	0.01	0.05	—	—	—	—	—	—
	6/20/57	7_4																				
Red River	6/17,18/56	4_2	—	—	0.05	—	0.01	—	0.01	—	—	—	—	—	—	—	—	—	0.01	0.01	—	—
	6/21/57	5_2																				
Do	6/18/56	5_3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	6/21/57	6_3																				
Bristol Bay:																						
Naknek weir	7/6,8/56	5_3	—	—	0.05	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	7/3–29/57	6_3																				
Egegik weir	7/17/56	4_2	—	—	0.05	—	—	—	—	—	—	—	—	—	0.01	—	—	—	—	—	—	—
	7/13/57	5_2																				
Do	7/17/56	5_3	—	—	—	—	—	—	—	—	—	0.05	—	—	0.05	—	—	—	0.05	—	—	—
	7/13/57	6_3																				
Ugashik weir	7/23/56	4_2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	7/19/57	5_2																				
Kvichak River	7/13/56	4_2	—	0.05	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	7/9/57	5_2																				
Do	7/13/56	4_2	—	—	0.05	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.05	—
	7/10/57	5_2																				
Wood River	7/11/56	4_2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	7/17/57	5_2																				
Combination of probability test			—	—	0.01	—	—	—	—	—	—	—	—	—	0.01	—	—	—	0.05	—	—	—

Results of these tests have given no indication of the effect of ocean age on the meristic characters included, except in the number of scales below the lateral line and in the number of branchiostegal rays and dorsal-fin elements.

Tests for Effects of Brood-year Differences

Since effects of variation in environmental factors on meristic characters have been demonstrated for many species of fish, the effect of differences in brood year on meristic characters was evaluated, using fish of the same total age but captured in successive years. The combined probability tests again show significant differences in mean number of scales below the lateral line, number of branchiostegal rays, and number of dorsal-fin elements, and, in addition in the number of pectoral-fin rays (Table 11).

Tests for Effects of Time of Sampling Within Streams

Samples available for evaluating the differences that might occur as runs progressed were limited to those obtained at Karluk River and Red River in Kodiak, Chignik River on the Alaska Peninsula, and Naknek River in Bristol Bay. Dates of sampling were categorized by dominant total age groups only (Table 12).

In 1955, differences in means between sampling times in any of the ten meristic characters were not indicated for Karluk River. In 1956, differences significant at the 1-percent level occurred in the number of dorsal-fin elements in the 4_2 group from Red River.

Some evidence of heterogeneity in populations was indicated in successive samples of red salmon of age group 5_2 from Chignik, where differences in means occurred in the number of scales below the lateral line, the position of the first haemal arch, and in the number of anal-fin elements.

TABLE 11. Analysis of variance for effects of brood-year differences and tests for common variance, in red salmon collected in 1955 to 1957. [Dash (—) indicates nonsignificant value]

Area	Date	Age group	Significance level for — Scales along lateral line		Scales below lateral line		Total vertebrae		First haemal arch		Ventral gill rakers		Total gill rakers		Branchiostegal rays		Pectoral-fin rays		Dorsal-fin elements		Anal-fin elements	
			Means	Variance	Means	Variance	Means	Variance	Means	Variance	Means	Variance	Means	Variance	Means	Variance	Means	Variance	Means	Variance	Means	Variance
Kodiak Island:																						
Karluk weir	{6/16, 29/55 6/22/56}	6_3	—	—	—	—	—	—	—	0.05	—	—	—	0.05	—	—	0.01	—	—	—		
Do	{6/16, 29/55 6/22/56}	6_4	—	—	—	—	—	—	—	—	—	—	—	—	0.05		—			—		—
Do	{6/22/56 6/20/57}	5_3	—	0.05	—	—	—	—	—	—	—	—						—	—		—	—
Do	{8/24/55 9/7/56 8/21/57 9/9, 17/57}	6_4	—	—	0.01	—	—	0.05	—	—	—	—	—	—	—	—	—	—	—	—	—	0.05
Do	{8/21/57 9/9, 17/57}	5_3	—	—	—	0.01	—	—	—	—	—	—	—	—	—	—	—	—	0.05		—	
Red River	{6/18/55 6/17, 18/56 6/21/57}	6_3	—		—		—			—	—			—			—					
Do	{6/18/56 6/21/57}	5_3		—	—				—	—			—	—			—				—	
Bristol Bay:																						
Egegik weir	{7/17/56 7/13/57}	5_2	—	—	—	0.05	—	—	0.05		—	—	—					—				
Do	{7/17/56 7/13/57}	5_3	—	0.05	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.01	0.05
Do	{7/17/56 7/13/57}	6_3	—	—	—	—	—	—	—	0.05	—	—	—	—	—	—	—	—	0.05	—		—
Ugashik weir	{7/23/56 7/19/57}	4_2	—	—	0.05	—	—	—	—	—	—	—	—	—	—	0.05	—	—	0.05	0.05	—	—
Do	{7/23/56 7/19/57}	5_3		—											—	—	—	—				
Kvichak River	{7/13/56 7/10/57}	5_3	—	—	—	—	—	—	—	—	—	—	—	—	0.05	—	—			—		
Combination of probability test			—	—	0.05	—	—	—	—	—	—	—	—	—	0.05	—	0.05	—	0.01	—		

Thus, of 110 tests of differences in mean counts of ten meristic characters between sampling dates within areas, 4 tests resulted in significant values of F. These values occurred rather randomly and with the possible exception of the 5_2 category of the Chignik River, it appears that, in general, within the limits of the time and areas of sampling, no significant variation in the number of meristic elements was attributable to time of sampling.

Conclusions

A summary of the results of all tests assessing the extent of internal variation in meristic characters within samples of red salmon collected in several streams in North America in 1955, 1956, and 1957 is shown in Table 13.

Significant differences were indicated in results of the combined probability tests for the effects of sex, fresh-water age, ocean age, and brood year in number of scale rows below the lateral line, branchiostegal rays, dorsal-fin elements, and anal-fin elements. From the data at hand the specific cause or causes of these differences cannot be isolated. The differences may be attributable to several factors—

1. The results may be an actual measure of differences effected in these specific characters by sex, fresh-water age, ocean age, or brood year.

TABLE 12. Analysis of variance for effects of different sampling dates and tests for common variance, in red salmon collected in 1955 to 1957. [Dash (—) indicates nonsignificant value]

Area	Date	Age group	Significance level for — Scales along lateral line: Means	Scales along lateral line: Variance	Scales below lateral line: Means	Scales below lateral line: Variance	Total vertebrae: Means	Total vertebrae: Variance	First haemal arch: Means	First haemal arch: Variance	Ventral gill rakers: Means	Ventral gill rakers: Variance	Total gill rakers: Means	Total gill rakers: Variance	Branchiostegal rays: Means	Branchiostegal rays: Variance	Pectoral-fin rays: Means	Pectoral-fin rays: Variance	Dorsal-fin elements: Means	Dorsal-fin elements: Variance	Anal-fin elements: Means	Anal-fin elements: Variance
1955:																						
Karluk weir	6/16, 6/29	6_4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1956:																						
Red River	6/17, 6/18	4_2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.01	—	—	-
Naknek weir	7/6, 7/8	5_2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	-
Do	7/6, 7/8	6_3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.05	—	—	—	—
1957:																						
Chignik weir	7/26, 7/27, 7/28	5_2	—	—	0.05	—	—	—	0.05	—	—	—	—	—	—	—	—	—	—	—	0.01	-
Do	7/25, 7/27, 7/28	6_3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Karluk weir	8/21, 9/9, 9/17	5_3	—	—	—	0.01	—	—	—	-	—	—	—	—	—	—	—	—	—	—	—	—
Do	8/21, 9/17	6_4	—	-	—	—	-	—	—	-	—	—	—	-	—	—	—	—	—	—	-	—
Naknek weir	7/3, 7/5, 7/11, 7/12, 7/23	5_2	—	—	—	—	—	—	—	—	—	0.05	—	0.05	—	—	—	—	—	—	—	—
Do	7/3, 7/5, 7/11, 7/12, 7/21, 7/25, 7/29	6_3	—	0.01	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Kvichak River	7/4, 7/10	5_2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	-

2. The differences may be attributable to a confounding effect resulting from representation of two or more within-stream subpopulations in our samples, each differing with respect to number of scales below the lateral line, branchiostegals, and dorsal-fin elements.

3. Since experimental evidence has shown that environment as well as genetics influences the fixation of meristic characters in salmonoids (Tåning, 1944; Seymour, 1956), it is possible that the individuals, even within a genetically related population (those from a particular spawning site), experienced very different environments during embryonic development which resulted in the differences indicated by our analyses.

In general, although the number of observations in some categories was small, the consistency of the results indicates that the effects of the different possible sources of variation were properly measured.

From the results of the combined probability tests we concluded that a confounding effect of three or four internal sources of variation occurred in the number of scales below the lateral line, number of dorsal-fin elements, and number of branchiostegal rays. After these three characters were discarded,

TABLE 13. Summary of all tests for intra-area sources of variations in meristic characters, in red salmon collected in 1955 to 1957.

Character	Number of significant effects found for —							
	Sexual dimorphism		Time of sampling			Fresh-water age	Ocean age	Brood year
	1956	1957	1955	1956	1957			
Scales along lateral line	1	1	0	0	0	0	1	0
Scales below lateral line	0	[1]2	0	0	1	[2]2	[2]4	[1]2
Total vertebrae	0	1	0	0	0	1	1	0
First haemal arch	0	1	0	0	1	0	1	1
Ventral gill rakers	1	1	0	0	0	0	1	0
Total gill rakers	0	0	0	0	0	0	1	0
Branchiostegal rays	1	2	0	0	0	[1]2	[2]3	[1]2
Pectoral-fin rays	2	0	0	0	0	1	0	[1]1
Dorsal-fin elements	1	2	0	1	0	[2]3	[1]2	[2]3
Anal-fin elements	2	0	0	0	1	[1]2	1	1
Number of tests for each character	16	17	1	3	7	9	11	13

[1] Combination of probability test result significant at 5-percent level.
[2] Combination of probability test result significant at 1-percent level.

ne components obtained from each stream sample ere homogeneous and the following statements may e made concerning the basic population unit, which ill be used in subsequent analyses:

1. The principal North American red salmon opulations are represented by entire samples obtained ithin river systems. These populations may be orphologically defined by the following characters:

Number of scales along the lateral line.
Total number of vertebrae.
Position of the first haemal arch.
Number of left-ventral gill rakers.
Total number of left gill rakers.
Number of pectoral-fin rays.
Number of anal-fin elements.

Subsequent analysis may show that any one or everal of these characters do not contribute appreciably to the separation between stream populaions. Retention of such characters cannot have any dverse effect on the results. Where a character may e foreseen to be a poor character for racial separaion, however, it will be discarded.

2. With the population so defined, in general, ithin limits of the years sampled, there were no ndications of intra-area differences in their meristic haracters between brood years. Thus, for a given rea included in the foregoing analysis, collections obained in any one year or in all the years of sampling ay be considered to define the meristic character of hat stream population. Pectoral-fin rays exhibited ignificance in the combined probability tests for brood years. An examination of the results of individual brood-year tests for this character shows that the significance was attributable entirely to differences in means between the 6_3 groups of 1955 and 1956 from Karluk River. The retention of a minimum number of useful characters enhances the efficiency of the multivariate analytical technique. Therefore, the number of pectoral-fin rays was retained and utilized pending an evaluation of its effect in subsequent analyses.

No samples were obtained within streams of Asia. The best available sample of Asian red salmon was collected by the Japanese mothership fishery in the Okhotsk Sea. Since these samples cannot be related to specific streams, nor can the individuals be assumed to be from a common stream population, detailed examination of the intra-population variations in meristic characters was not attempted. The desirability of having samples from Asian streams is recognized and attempts are being made to obtain them for future analyses. However, the major populations of Asian red salmon will be represented by the Okhotsk Sea samples, morphologically defined by the same characters listed for the North American intracontinental standards.

CORRELATION OF SELECTED CHARACTERS WITH LENGTH OF FISH

Various types of gear were used in collecting specimens for these studies, and may have selected fish according to size. To evaluate a possible bias in distribution of meristic characters due to their association with length, correlation of the seven selected meristic characters with fish length was examined. For this

TABLE 14. Correlation coefficients of each meristic character with length, in red salmon, 1955–57.

Area	Number of fish	Scales along lateral line	Total vertebrae	First haemal arch	Ventral gill rakers	Total gill rakers	Pectoral-fin rays	Anal-fin elements
1955:								
Karluk River	185	[1]0.295	[2]0.184	0.051	[2]0.200	[1]0.216	[2]0.159	−0.001
Red River	52	0.267	[2]0.301	[2]0.278	0.231	[2]0.287	0.055	0.010
Fraser River:								
Cultus Lake	59	−0.229	−0.232	−0.055	0.137	0.200	0.071	−0.016
Adams River	60	0.241	[1]0.379	[1]0.356	0.142	0.110	0.125	0.121
Naknek River	46	0.081	−0.105	0.021	0.182	0.217	−0.202	0.066
Attu Island	41	0.220	0.147	−0.098	0.009	0.038	0.258	−0.217
1956:								
Naknek weir	183	0.004	−0.039	0.001	−0.072	−0.010	0.050	0.122
Egegik weir	198	0.062	−0.007	−0.085	[2]0.146	[2]0.156	0.031	0.022
Ugashik weir	187	0.085	0.019	0.085	0.114	[1]0.216	0.123	−0.071
Wood River	187	[1]0.322	[2]0.169	0.117	[2]0.173	[1]0.201	0.107	0.037
Kvichak River	185	[1]0.329	[1]0.315	0.085	0.116	0.108	0.074	0.135
Okhotsk Sea	132	0.016	0.040	[1]0.251	0.040	0.047	[2]−0.180	0.072
Do	167	[2]0.156	0.143	−0.056	0.135	[2]0.157	0.024	0.149
Do	187	0.078	0.113	0.114	0.012	0.036	0.092	0.054
Do	69	−0.020	0.105	−0.034	−0.123	−0.035	−0.046	−0.083
Adak Island	215	[2]0.142	0.070	0.006	[2]0.135	[1]0.190	0.070	0.112
Karluk River	187	0.136	0.074	0.036	[1]0.196	[1]0.236	0.079	−0.077
Red River	188	[2]0.178	0.128	0.047	0.075	[1]0.186	−0.024	0.078
Do	182	[2]0.205	0.122	0.026	−0.044	−0.064	0.005	0.141
Attu Island	219	[2]0.137	0.061	0.069	0.020	0.018	0.064	0.120
Do	88	0.144	0.018	−0.068	−0.006	−0.033	0.131	[2]0.253
Do	42	0.290	0.105	0.273	0.128	0.144	−0.205	0.255
1957:								
Naknek River	93	0.194	0.056	0.034	−0.146	−0.117	−0.068	−0.090
Do	93	−0.046	−0.004	0.057	[2]0.231	0.164	−0.006	0.047
Do	56	0.206	0.163	−0.086	0.080	0.059	−0.043	0.004
Do	94	0.184	0.043	−0.043	[1]0.269	[1]0.307	0.006	0.040
Do	49	0.131	[2]0.304	−0.030	[1]0.424	[1]0.428	0.210	0.096
Do	96	0.068	0.063	−0.070	−0.101	−0.042	−0.053	0.107
Egegik River	180	0.130	0.066	0.082	0.063	0.089	−0.080	−0.187
Ugashik River	184	0.054	−0.016	−0.018	−0.052	−0.064	−0.128	0.095
Wood River	163	0.137	−0.092	−0.108	0.051	0.082	0.069	−0.126
Kvichak River	94	0.051	0.023	−0.149	−0.003	−0.008	−0.004	0.114
Do	90	0.059	0.089	0.002	−0.126	−0.116	−0.186	0.002
Okhotsk Sea	192	0.016	0.035	−0.043	−0.049	−0.018	−0.081	0.138
Do	195	[1]0.281	[1]0.236	0.073	−0.059	−0.005	0.006	−0.022
Do	194	−0.032	−0.014	−0.082	[2]−0.044	[2]−0.154	−0.034	0.005
Karluk River	93	0.051	0.083	−0.050	−0.032	0.103	−0.028	−0.008
Do	105	0.174	[1]0.347	[2]0.227	−0.078	−0.042	0.095	−0.049
Do	94	0.129	0.076	0.005	−0.129	−0.132	−0.106	0.081
Do	117	0.077	−0.066	−0.009	0.116	0.112	−0.062	0.071
Red River	193	[1]0.204	[2]0.171	0.104	−0.075	0.016	0.054	−0.075
Columbia River	53	[2]0.318	0.205	0.037	[2]0.286	0.212	−0.070	0.105
Do	46	−0.167	0.120	−0.100	−0.284	−0.256	−0.076	−0.201
Chignik River	42	−0.002	−0.141	−0.026	[2]−0.311	[2]−0.349	0.102	0.091
Do	39	[2]0.315	0.182	0.131	−0.110	0.018	−0.070	0.126
Do	57	0.051	0.030	−0.101	0.099	0.174	−0.041	0.113
Do	52	−0.110	−0.059	0.100	0.079	0.036	0.331	0.070
ρ*	5,723	0.131	0.087	0.030	0.042	0.074	0.018	0.043
ρ^2		0.017	0.008	0.001	0.002	0.005	0.000	0.002

[1] Significant at 1-percent level.

[2] Significant at 5-percent level.

* ρ is an estimated population correlation coefficient (null hypothesis: $\rho=0$).

ırpose, stream samples were used, and collections in e different years were treated both separately and mbined. The three characters previously shown to affected by other sources of variation were elimiıted. The correlation analyses of meristic characters length for the 1955, 1956, and 1957 collections are own in Table 14.

The expression $100\rho^2$ may be said to be an approximate measure of the variability in the observations for a particular character due to corresponding variability in length. This variability is about 2 percent at the maximum (scales along the lateral line with length). Further, on the basis of these results it seems reasonable to conclude that correlation between length and any of the characters with which we are here concerned was negligible.

PROBLEM II. CLASSIFICATION OF HIGH-SEAS RED SALMON TO CONTINENT OF ORIGIN

Having established a basic within-stream popula-on unit in which the various components are homo-eneous with respect to seven meristic characters, we ıall consider the statistical treatment of these data ıat will enable us to allocate red salmon taken on the igh seas to their continent of origin. Several clasficatory techniques are available for this purpose. 'he method that we shall use in this report is the dis-riminant function analysis (Fisher, 1936).

Discriminant function analysis is a multivariate atistical technique that can be used to classify indiidual salmon to their native streams on the basis of selected set of variates. This procedure is optimal, e., it minimizes the two probabilities of misclassifica-on when these variates are used, if the variates have jointly multivariate normal distribution in each popılation and a common dispersion matrix (common ariances and covariances among groups). Secondly, ıe stream populations composing the high-seas samles must be known. Therefore, the classification of ılmon taken on the high seas by discriminant func-on analysis will be developed in the following ıanner:

1. Select the areas for inclusion in the function ıat contribute red salmon to the high-seas popula-ions represented in our collections.

2. Determine the extent to which distribution of ıe seven meristic characters satisfies the requirements or optimal use of the discriminant function.

3. Test empirically the efficacy of the discriminant unction.

4. Apply the discriminant function, classifying pecimens from the high-seas samples to their areas of rigin. In both 1956 and 1957, almost all high-seas amples were obtained west of longitude 160°W. and rimarily west of 170°W. between latitudes 50°N. and 0°N. (Figs. 2 and 3).

SELECTION OF AREAS

A primary consideration in the use of the discriminant function analysis is establishing which North American and Asian streams or regions contribute to the red salmon populations distributed in the high-seas waters of the North Pacific Ocean and Bering Sea. Initially, this question may be considered on intuitive premises.

A large share of the salmon distributed on the high seas are probably from a relatively few red salmon streams of North America and Asia. For this reason alone, these principal contributors should be included in the function. The most productive red salmon streams in Alaska are the five principal river systems of Bristol Bay as a group (Table 5). The Fraser River is the principal red salmon contributor in British Columbia (Table 6). Similarly, the principal Asian catches of red salmon are from streams on the southwestern coast of Kamchatka (Table 7).

The presence of fish from Bristol Bay, Chignik River, and southwestern Kamchatka populations in the high-seas samples can be demonstrated by direct evidence for the area west of longitude 170°W. in the North Pacific Ocean and Bering Sea. Red salmon tagging experiments conducted under the auspices of the International North Pacific Fisheries Commission have produced tag returns from the estuarine fisheries of Bristol Bay and the Alaska Peninsula and from the Japanese high-seas fishery (International North Pacific Fisheries Commission, 1958). Although the origin of those red salmon recovered by the Japanese high-seas fishery can only be conjectured, significant in these results is the lack of evidence that red salmon from other North American systems occur in the Aleutian Islands area within limits of time and areas of tagging.

From samples obtained at times and places comparable with those used in our analysis, Margolis

(1958) found red salmon taken in ocean waters north and south of the Aleutian Islands to be infected with *Triaenophorus* and *Dacnitis*. Both parasites are contracted by salmon in their fresh-water habitat and each has very restricted distribution: *Triaenophorus* principally in Wood River, Naknek River, Ugashik River, and Kuskokwim River, Alaska; and *Dacnitis* in Kamchatka. Since not all red salmon of these populations nor all those taken on the high seas were infected, the areas of origin of the noninfected individuals have not been determined; however, it is significant that a method independent of tagging has confirmed the presence of Bristol Bay and Kamchatka red salmon in the area.

On this evidence, the analyses which follow will assume that most specimens in the high-seas samples to be classified are of western Alaska or southwestern Kamchatka origin. The southwestern Kamchatka population will be represented by samples obtained from the Japanese fishery in the Okhotsk Sea. Western Alaska will be represented by samples from the principal streams of Bristol Bay, the Chignik River (Alaska Peninsula), and Karluk and Red Rivers (Kodiak Island), each sample weighted according to relative abundance as estimated by escapements to these systems.

The lack of direct evidence of red salmon from areas other than the two mentioned does not necessarily preclude their presence. Should red salmon from these areas occur in quantity, their presence would introduce a source of error in our classificatory results. This possibility is considered in a later section of this report.

The high-seas samples to be classified contain immature as well as mature specimens. Ishida and Miyaguchi (1958) and Godfrey (1959) have developed criteria for sexual maturity using gonad weights. But, since it was felt that these criteria might not be adequate for determining sexual maturity of salmon taken in May and early June, specimens from high-seas samples were classified without regard to degree of sexual maturity.

CONSTRUCTION OF THE DISCRIMINANT FUNCTION

Since its introduction by Fisher (1936), the method of discriminant functions has been found extremely useful in deriving test criteria for discriminating between any two chosen classes, such as racial groups, the sexes, and so on. Hill (1959) constructed a discriminant function that classified correctly about 81 percent of a mixed population of Hudson and Connecticut River shad based on six meristic characters. In general, the problem is to select the best linear function of each of the several original variables whose coefficients will maximize the value of a statistic to be used. Thus, the multivariate data are reduced to a univariate case and an appropriate discriminating rule can be established to classify individuals to their respective populations.

Consider a linear combination of the measurements

$$Y=\sum_{i=1}^{k} l_i X_i$$

where X_i is the value of the i^{th} character with corresponding coefficient l_i. For red salmon, we have, then

$$Y=l_1X_1+l_2X_2+l_3X_3+l_4X_4+l_5X_5+l_6X_6+l_7X_7$$

where X_1 is the number of scales along the lateral line, X_2 the total number of vertebrae, X_3 the position of the first haemal arch, X_4 the number of ventral gill rakers, X_5 the total number of gill rakers, X_6 the number of pectoral-fin rays, and X_7 the number of anal-fin elements. Rao (1952) has shown that the best linear compound for two multivariate normal populations is such that the constants l_i are obtained by solving the following set of equations:

$$\begin{aligned} &l_1w_{11}+l_2w_{12}+l_3w_{13}+l_4w_{14}+l_5w_{15}+l_6w_{16}+l_7w_{17}=d_1\\ &l_1w_{21}+l_2w_{22}\ \ldots\qquad\qquad\qquad\qquad\qquad\quad =d_2\\ &\qquad\cdot\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\quad\ \cdot\\ &\qquad\cdot\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\quad\ \cdot\\ &l_1w_{71}+l_2w_{72}\ \ldots\qquad\qquad\qquad\qquad\qquad\quad l_7w_{77}=d_7 \end{aligned}$$

d_i is the difference between the estimated population means of the i^{th} character, and w_{ij} is the pooled covariance between the i^{th} and j^{th} characters. The w_{ij} are estimated from the following equation:

$$(N_a+N_b-2)\,w_{ij}=\sum_{k=1}^{Na}(X_{iak}-\bar{X}_{ia})(X_{jak}-\bar{X}_{ja})$$

$$+\sum_{k=1}^{Nb}(X_{ibk}-\bar{X}_{ib})\,(X_{jbk}-\bar{X}_{jb})$$

where N_a and N_b are the sample sizes from the western Alaska (Bristol Bay tributaries, Kodiak Island, and Chignik River) population and southwestern Kamchatka population, respectively. X_{iak} is the value of the i^{th} character for the k^{th} fish from the western Alaska population. $\bar{X}_{ia}$ is the mean value of the i^{th} character for the western Alaska population.

In setting up rules for classification, the critical value will be $Y_0=\frac{1}{2}(\bar{Y}_a+\bar{Y}_b)$ where $\bar{Y}_a$ is the estimated mean value of the discriminant function for the western Alaska population and $\bar{Y}_b$ for the southwestern Kamchatka population. If the value of (Y) of the discriminant function for an individual to be classified is

er than Y_0, it will be assigned to one population, ss, it will be assigned to the other. The variance V is D^2 and is given by—

$$D^2 = l_1d_1 + l_2d_2 + l_3d_3 + l_4d_4 + l_5d_5 + l_6d_6 + l_7d_7.$$

When the discriminant function is used in the ıner described, the probability of correctly assign- an individual fish to its native population is the ıe for each population. Rao (1952) has shown that probability is equal to the probability that a mal deviate with mean zero and standard deviation l will be less than or equal to $^1/_2D$.

From the table of variances and covariances (dis- sion matrix in Appendix C) which was constructed n the meristic data obtained from red salmon ected in 1956 in the Okhotsk Sea and western ıska, the following set of equations was obtained:

$$96657\, l_1 + 1.169526\, l_2 + 0.558848\, l_3 + 0.148560\, l_4$$
$$+0.282691\, l_5 + 0.061674\, l_6 + 0.177691\, l_7 = 1.052880$$
$$69526\, l_1 + 0.774348\, l_2 \quad . \quad . \quad . \qquad = 0.215575$$
$$\cdot \quad \cdot \quad \cdot \qquad \cdot$$
$$\cdot \quad \cdot \quad \cdot \qquad \cdot$$
$$77691\, l_1 + \quad . \quad . \quad . \quad . \qquad +0.395240\, l_7 = 0.072219.$$

Rao's (1952) method was used for solving these equations so that successive discriminant functions were obtained. First a discriminant function was computed by using only the number of scales along the lateral line. The second discriminant function was obtained by using both the number of scales along the lateral line and the total number of vertebrae. An additional character was used for each successive step. Thus, by using all seven meristic characters the final discriminant function was obtained at the last stage of the computation. The essential computational stages of constructing the discriminant function are presented in Appendix C. Table 15 lists successive D_i^2 values with corresponding l_i. By substituting the value of l_i into the function $Y = \sum_{i=1}^{k} l_i X_i$, the discriminant function for k number of characters can be obtained.

Thus, (from Table 15) the discriminant function using all seven meristic characters is—

$$Y = .2643\, X_1 - .3968\, X_2 + .4214\, X_3 - .4715\, X_4$$
$$+ .9086\, X_5 + 1.5755\, X_6 - .0340\, X_7.$$

TABLE 15. Coefficients of discriminant function $Y_i = \sum_{i=1}^{k} l_i X_i$ and successive values of D_i^2.

l_1	l_2	l_3	l_4	l_5	l_6	l_7	D_i^2	$P=(D_i/2)$
.277318							0.291983	0.606
.358220	0.262636						0.320546	0.612
.345131	-0.427990	0.434965					0.426193	0.628
.311158	-0.427608	0.470236	0.732531				0.917038	0.683
.281835	-0.405781	0.457901	-0.500529	0.975918			1.416147	0.724
.263549	-0.399980	0.422957	-0.471359	0.907888	1.573787		2.247130	0.773
.264321	-0.396849	0.421494	-0.471575	0.908622	1.575538	-0.034089	2.247575	0.773

e estimated mean values of the coefficients of the criminant function for the western Alaska popula- n ($\bar{Y}_a$) and the southwestern Kamchatka popula- n ($\bar{Y}_b$) were determined by substituting $\bar{X}_i$, the an counts of each of the seven meristic characters each population, into the function. Tabulation these means is given in Table 16.

From the dispersion matrix in Appendix C, the ues of $\bar{Y}_a$ and $\bar{Y}_b$ are 70.432 for the western Alaska pulation and 68.184 for the southwestern Kam- atka population. Therefore, in discriminating be- een the two populations, those fish with a value of less than 69.308 (Y_0) are considered as being from uthwestern Kamchatka and those with values of ore than 69.308 are assigned to the western Alaska pulation. Since D^2 for the function is 2.248, the obability of misclassification is approximately 22.7 rcent. This error of classification would be the proportion of the western Alaska fish having Y values less than 69.308 and the proportion of the south western Kamchatka fish having Y values more than 69.308.

EMPIRICAL TEST OF THE DISCRIMINANT FUNCTION

Although the discriminant function analysis is well established in theory, its suitability and efficacy with respect to red salmon meristic data were tested empirically. Since previous analyses showed no brood-year differences for seven meristic characters in the areas considered, samples of red salmon collected in 1957, from Bristol Bay tributaries, Kodiak Island, Chignik River and Okhotsk Sea were classified using the function—

$$Y = .2643\, X_1 - .3968\, X_2 + .4214\, X_3 - .4715\, X_4$$
$$+ .9086\, X_5 + 1.5755\, X_6 - .0340\, X_7$$

TABLE 16. Mean values of seven meristic characters in red salmon, for areas used in constructing the discriminant function.
[Based on fish collected in 1956]

Area	Scales along lateral line	Vertebrae	First haemal arch	Ventral gill rakers	Gill rakers	Pectoral-fin rays	Anal-fin elements
Bristol Bay:							
Naknek River	130.4208	67.4317	34.5519	22.9454	37.0273	16.2186	17.918
Egegik River	130.0909	67.2475	34.4949	23.0051	37.2525	16.5101	17.939
Ugashik River	130.1658	67.2995	34.5241	22.8930	37.0214	16.4973	17.914
Kvichak River	131.0484	67.4892	34.7204	23.0538	37.3441	16.4892	17.914
Wood River	129.9947	67.2910	34.3862	22.7249	36.6243	16.3704	17.978
Kodiak Island:							
Karluk River	130.2674	67.0856	34.5508	22.5080	36.3476	16.4866	17.882
Do	130.9101	67.3968	34.4815	22.7460	36.6614	16.6190	17.994
Red River	130.8571	67.3626	34.4396	22.7747	36.8901	16.4945	18.225
Chignik:							
Chignik River	131.7128	67.7234	34.8404	23.0213	37.1064	16.4043	18.095
Average mean, western Alaska population	130.6076	67.3697	34.5544	22.8525	36.9195	16.4544	17.984
Okhotsk Sea:							
51°49′ N., 154°06′ E	129.4697	67.1212	34.1894	22.1742	35.6212	15.7652	18.022
52°08′ N., 154°32′ E	129.7059	67.2032	34.1337	22.1337	35.4599	15.9037	17.834
51°55′ N., 154°13′ E	129.6228	67.1617	34.1497	22.1796	35.5030	15.8802	17.880
51°22′ N., 153°51′ E	129.4203	67.1304	34.3188	22.1159	35.3768	15.8841	17.913
Average mean, southwestern Kamchatka population	129.5547	67.1541	34.1979	22.1508	35.4902	15.8583	17.912

which was constructed with data obtained from red salmon taken in these same areas in 1956.

The resulting frequencies of Y values above and below 69.308 are listed in Table 17. It can be seen that the percentage of misclassification of 1957 fish of any given population was in close agreement with the values resulting from classifying the 1956 sample from that same area. Furthermore, the errors of misclassification for both populations (approximately 22 percent for western Alaska red salmon and 23 percent for southwestern Kamchatka fish) were comparable with the theoretical 22.7-percent average error of misclassification inherent to the function.

This result is significant not only as empirical evidence of the efficacy of the function but it also provides a direct assessment of the error of misclassification, since the fish classified (1957 collection) were obtained independently of those used in constructing the function.

The expected 22.7-percent misclassification represents the maximum bias that would occur in the estimates of western Alaska and southwestern Kamchatka fish when a sample is composed of fish from one population only. An increasing degree of intermingling of the two populations within a sample would proportionally decrease this error. If equal numbers of western Alaska and southwestern Kamchatka fish wer present in a sample, the errors of misclassificatio would be cancelled and the bias reduced to zero.

If it is assumed that P_A and P_B are the probabilitie of misclassifying fish from the western Alaska an southwestern Kamchatka populations, respectively the bias can be easily corrected. Suppose a high-sea sample consists of N fish of which N_A are the weste Alaska fish and N_B are the southwestern Kamchatk fish, while R_A and R_B are the numbers of fish classifie to the western Alaska and southwestern Kamchatk populations by discriminant function analysis. The R_A will consist of $P_B N_B$ fish that were misclassified a western Alaska fish and $(1-P_A)N_A$ fish that were cor rectly classified.

Symbolically:

$$P_B N_B + (1-P_A)N_A = R_A,$$

and similarly,

$$P_A N_A + (1-P_B)N_B = R_B,$$

where

$$R_A + R_B = N = N_A + N_B.$$

Subsequently, we have

$$\frac{N_A}{N} = \frac{R_A}{P_B - N} \cdot \frac{}{P_A + P_B - 1}$$

he expression $\frac{100N_A}{N}$ represents the corrected :entage of western Alaska red salmon present in sample.

n assessing the probability of misclassifying fish n the western Alaska population, ideally the errors nisclassification should be weighted according to relative abundance of the various constituent ulations composing each high-seas sample. In absence of such information, the best estimate is average error of misclassification weighted according to the relative abundance of fish from various areas which compose the western Alaska population (Table 18). The relative abundance is calculated from the escapement data of 1956 and 1957 while the errors of misclassification (tabulated in the third column of Table 18) are obtained by applying the discriminant function to the 1957 samples. As a result, the computed average value of P_A is 17.8 percent.[1]

BLE 17. Frequency of the values (Y) of the discriminant unction above and below the critical value 69.308 (Y_0) or samples from western Alaska and southwestern Kamhatka, 1956–57.

rea	Sampling date	Size of sample	Frequency $Y > Y_0$[1]	Frequency $Y < Y_0$[2]	Percent $Y > Y_0$[1]	Percent $Y < Y_0$[2]
:						
tol Bay :						
knek River	7/8	182	127	55	69.8	30.2
egik River	7/17	198	167	31	84.3	15.7
gashik River	7/23	187	154	33	82.4	17.6
ichak River	7/13	180	153	27	85.0	15.0
od River	7/11	196	127	69	64.8	35.2
diak Island :						
rluk River	6/22	187	129	58	69.0	31.0
rluk River	9/7	175	133	42	76.0	24.0
d River	6/18	196	159	37	81.1	18.9
gnik :						
ignik River	8/2	94	74	20	78.7	21.3
otsk Sea :						
°49′ N., 154°06′ E	6/21	132	29	103	22.0	78.0
°08′ N., 154°32′ E	6/28	187	39	148	20.4	79.6
°55′ N., 154°13′ E	7/6	168	40	128	23.8	76.2
°22′ N., 153°51′ E	7/13	69	18	51	26.1	73.9
:						
tol Bay :						
knek River	7/3	508	398	110	78.4	21.6
egik River	7/13	180	146	34	81.1	18.9
gashik River	7/19	184	143	41	77.7	23.3
ichak River	7/9	184	156	28	84.8	15.2
od River	7/17	164	97	67	59.2	40.8
diak Island :						
rluk River	6/20	93	66	27	71.0	29.0
rluk River	8/21	316	251	65	79.4	20.6
d River	6/21	193	168	25	87.1	12.9
gnik :						
ignik River	7/25	190	166	24	87.4	12.6
otsk Sea :						
°08′ N., 154°15′ E	6/24	192	48	144	25.0	75.0
°52′ N., 153°28′ E	7/4	195	50	145	25.6	74.4
°16′ N., 153°39′ E	7/14	194	40	154	20.6	79.4

Western Alaska type.
Southwestern Kamchatka type.

TABLE 18. Average error of classification of red salmon weighted according to relative abundance of contributing stocks, western Alaska, 1956–57.

Area	Escapement in 1956 and 1957 (millions)	Relative abundance	Observed misclassification (percent)	Weighted value
Naknek	2.406	0.1212	21.6	2.6158
Egegik	1.493	0.0752	18.9	1.4213
Ugashik	0.636	0.0320	22.3	0.7136
Kvichak	12.407	0.6247	15.2	9.4954
Wood River	1.070	0.0539	40.8	2.1991
Karluk River	0.357	0.0180	22.5	0.4050
Red River	0.225	0.0113	12.9	0.1458
Chignik	1.265	0.0637	12.6	0.8026
Total	19.859	1.0000		17.7988

SUMMARY

Average error of classification :
Western Alaska population $(P_A) = 17.7988\%$
Southwestern Kamchatka population

$$(P_B) = \frac{20.6+25.6+25.0}{3} = 23.7333\%$$

The probability of misclassifying the southwestern Kamchatka population is an average value of the three percentages obtained from the 1957 data, since information on the relative abundance of the contributing stocks is not available. Moreover, the values of error in misclassification obtained by applying the discriminant function to the 1957 sample were very similar (Table 17). The probability of misclassifying fish from the southwestern Kamchatka population (P_B) is 23.7 percent (Table 18).

Although the available supplementary evidence indicates that red salmon on the high seas north and south of the Aleutian Islands are of southwestern Kamchatka or western Alaska origin, red salmon from

[1] In preceding tests for the effects of brood year, age group 6_3 fish from Karluk showed significant differences in mean number of pectoral-fin rays for 1955, 1956, and 1957. In correcting the probabilities of misclassification for bias due to abundance, Karluk contributes only about 2 percent in the weighting. Therefore, the inclusion of pectoral-fin rays is thought not to affect the results significantly.

TABLE 19. Frequency of values of discriminant function (Y) above and below the critical value 69.308 (Y_0) for samples from North American inshore fisheries, 1956–57.

Area	Sampling date	Size of sample	Frequency $Y > Y_0$[1]	Frequency $Y < Y_0$[2]	Percent $Y > Y_0$[1]	Percent $Y < Y_0$[2]
1956:						
Attu Island	8/4	219	112	107	51.1	48.9
	8/28	88	42	46	47.7	52.3
	8/4	42	7	35	16.7	83.3
Adak Island	8/5	229	12	217	5.2	94.8
Unalaska Island	7/16	105	1	104	0.9	99.1
Alaska Peninsula	7/24	126	85	41	67.5	32.5
King Cove	6/26	26	21	5	80.8	19.2
Teller	7/17	42	20	22	47.6	52.4
Cook Inlet	7/25	150	11	139	7.3	92.7
	8/1	24	6	18	25.0	75.0
Copper River	6/15	209	43	166	20.6	79.4
Yakutat	8/4	77	17	60	22.1	77.9
Petersburg	7/13	19	1	18	5.3	94.7
	7/13	166	23	143	13.9	86.1
Ketchikan	7/13	16	3	13	18.8	81.2
	7/31	94	11	83	11.7	88.3
	8/2	74	6	68	8.1	91.9
Namu	4/–	49	5	44	10.2	89.8
Rivers Inlet	7/16	177	11	166	6.2	93.8
Skeena River	10/26	185	21	164	11.4	88.6
Nass River	8/6	92	20	72	21.7	78.3
Fraser River	8/7	192	87	105	45.3	54.7
Columbia River	7/2	70	8	62	11.4	88.6
	8/14	52	10	42	19.2	80.8
1957:						
Attu Island	7/4	58	31	27	53.4	46.6
	7/28	26	12	14	46.2	53.8
	7/2	19	10	9	52.6	47.4
	8/18	28	16	12	57.1	42.9
King Cove	6/22	62	9	11	82.3	17.7
	7/11	55	51	15	72.7	27.3
	7/26	76	40	30	60.5	39.5
Nome	7/26	50	24	26	48.0	52.0
Bethel	6/25	54	29	25	53.7	46.3
	6/27	39	25	14	64.1	35.9
Copper River	6/24	74	25	49	33.8	66.2
	7/16	41	7	34	17.1	82.9
	8/1	73	9	64	12.3	87.7
Yakutat	8/1	172	27	145	15.7	84.3
Petersburg	7/11	213	23	190	10.8	89.2
Ketchikan	7/15	11	1	10	9.1	90.9
	8/20	22	2	20	9.1	90.9
	8/14	37	3	34	8.1	91.9
	8/15	40	2	38	5.0	95.0
	8/16	42	4	38	9.5	90.5
	8/17	37	6	31	16.2	83.8
Rivers Inlet	–	83	9	74	10.8	89.2
Skeena River	7/19	99	20	79	20.2	79.8
	7/30	93	24	69	25.8	74.2
Nass River	7/4	90	26	64	28.9	71.1
Fraser River	8/1	67	25	42	37.3	62.7
	8/6	97	23	74	23.7	76.3
Columbia River	8/12	55	7	48	12.7	87.3
	8/14	47	12	35	25.5	74.5

[1] Western Alaska type.

[2] Southwestern Kamchatka type.

North American areas other than western Alaska ma have been present in specific areas. Consequentl samples collected in both 1956 and 1957 from Nort American streams and inshore fisheries other than tho of Bristol Bay, Kodiak, and Chignik were classifie using the calculated discriminant function. Th marked similarity of results with the 1956 and 195 samples is noted (Table 19). Both in 1956 and i 1957, samples collected from areas north of Brist Bay (Teller, Nome, and Bethel) tend to have high errors of misclassification as southwestern Kamchatk fish than do Bristol Bay samples. From Cook Inl southward all samples had very large percentages specimens misclassified as red salmon of southweste Kamchatka origin.

When k equals the number of characters, the di criminant function specifies the direction in k spac in which the populations are most distinct. In ou analysis we have seven characters, therefore, seve directions in space. Figure 5 (top) diagrams th morphological relationship of salmon from sever North American areas to those of Bristol Bay and soutl western Kamchatka in two dimensions. The mo phological dissimilarity between populations is direct

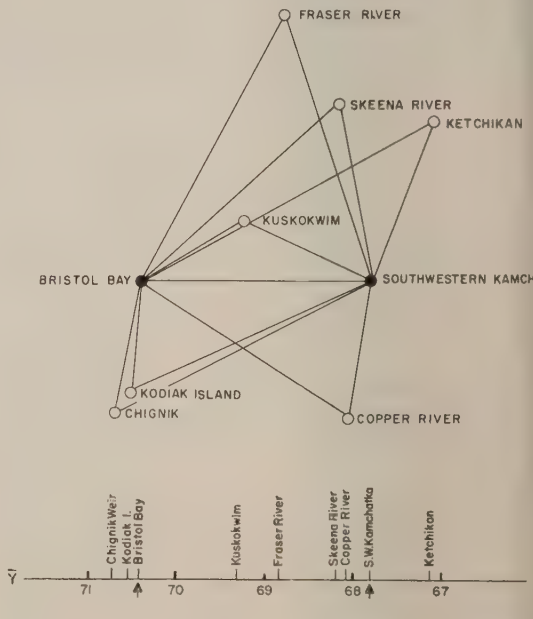

FIGURE 5. Top: Diagrammatic illustration of relationshi of certain North American samples of red salmon to thos of Bristol Bay and southwestern Kamchatka, using averag D values (distance function). Bottom: Mean values c the discriminant function between southwestern Kamchat ka and western Alaska and other North American popu lations.

TABLE 20. Variances of the seven meristic characters in red salmon, by areas, and results of Bartlett's test for homogeneity of variances. [Based on all areas used to construct discriminant function]

Area	Scales along lateral line	Vertebrae	First haemal arch	Ventral gill rakers	Gill rakers	Pectoral-fin rays	Anal-fin elements
Bristol Bay:							
Naknek River	5.2897	1.1480	0.8531	0.8433	1.6532	0.4027	0.4164
Egegik River	2.7645	0.5327	0.6272	0.9188	1.9869	0.3832	0.4025
Ugashik River	2.9892	0.4478	0.5520	0.9027	1.8705	0.2729	0.2831
Kvichak River	4.1553	0.7490	0.7214	0.7756	1.5677	0.3703	0.4035
Wood River	3.4214	0.6652	0.6640	0.9134	2.1510	0.3302	0.4465
Kodiak Island:							
Karluk River	3.0477	0.6056	0.6682	0.7889	1.7658	0.3157	0.3732
Do	4.5720	0.9112	0.7723	0.8820	2.1615	0.3330	0.3565
Red River	3.3169	0.6086	0.6897	0.8938	1.7451	0.3177	0.3855
Chignik:							
Chignik lagoon	4.2507	0.8692	0.6734	0.9889	2.3973	0.3295	0.3457
Okhotsk Sea:							
51°49′ N., 154°06′ E	3.9771	0.6724	0.6128	1.1374	2.4662	0.3185	0.3889
52°08′ N., 154°32′ E	3.9402	0.9591	0.8050	1.0629	2.3681	0.3348	0.5047
51°55′ N., 154°13′ E	4.2490	1.0886	0.7425	0.9796	2.0348	0.3472	0.4315
51°22′ N., 153°51′ E	3.7779	1.0566	0.6910	1.1335	2.6501	0.3394	0.3453
Character M-values	[1,2]37.9502	[3]86.7764	13.3088	11.1081	[2]23.2566	4.6032	19.2555

[1] $\chi^2_{.95}$ with (13–1) d.f.=21.03.
[2] Significant at 5-percent level.
[3] Significant at 1-percent level.

roportional to the distance between populations. The particular function discussed in this report utilizes ne one dimension in which the Bristol Bay and outhwestern Kamchatka populations are most dis-nct. As shown in the lower part of Figure 5, all oints in the upper part of the chart are then projected nto line $\overline{Y}$. The vertical dimension is thus eliminated nd the normalized means of other North American reas such as Fraser River, Skeena River, Copper iver, and Ketchikan occupy positions on line $\overline{Y}$ omparatively closer to southwestern Kamchatka than o Bristol Bay. As a consequence, the large errors of isclassifying red salmon from these areas as from outhwestern Kamchatka resulted as was shown in able 19. However, it can also be seen from Figure (top) that by selecting a function which utilizes nother dimension, separation of fish from south-estern Kamchatka and from these other North merican areas can be effected.

Therefore, in applying this particular discriminant nction, were red salmon native to North American reas other than western Alaska present in the high-as samples being classified, they more likely would e assigned to the southwestern Kamchatka popula-on rather than to the western Alaska population. hus, the percentage estimates in classification may be iased to varying degrees in favor of southwestern Kamchatka.

The technique of discriminant function analysis used in this study is based on several assumptions. Counts of the seven meristic characters must follow a multivariae normal distribution in each of the two populations with equal variances and covariances. Examination of the frequency distributions of the seven characters for each sample indicates no departures from normality (Appendix D, Figs. 1–7).

Bartlett's test for common variance in the seven meristic characters indicated probable discrepancies between variances in the number of scales along the lateral line, number of vertebrae, and number of gill rakers. The latter was barely significant at the 5-percent level. The variances ranged from 2.76 to 5.28 for the number of scales along the lateral line, from 0.44 to 1.14 for the number of vertebrae, and from 1.56 to 2.65 for the number of gill rakers (Table 20). Although these slight discrepancies among variances might tend to reduce the efficiency of the constructed discriminant function, in many instances the contribution of a character to separation of means exceeds this disadvantage. Results of the empirical test for the function (Table 17) have demonstrated that inclusion of the characters in question did not appreciably affect the efficiency of the function. On

TABLE 21. Discriminant function analysis: High-seas samples of red salmon, 1956.

Sample	Sampling date	Locality	Size of sample	Percent classified — Western Alaska	Southwestern Kamchatka	Percent corrected western Alaska
No. 1	6/21	154°06′ E., 51°49′N	132	21.97	78.03	00.00
No. 2	6/28	154°32′ E., 52°08′N	187	20.86	79.14	00.00
No. 3	7/6	154°13′ E., 51°55′N	168	23.81	76.19	00.21
No. 4	7/13	153°51′ E., 51°22′N	69	26.09	73.91	04.09
No. 5	8/5	159°50′ E., 51°40′N	166	28.92	71.08	08.92
No. 6	7/25	163°08′ E., 51°04′N	163	26.38	73.62	04.58
No. 7	6/5	170°52′ E., 52°08′N	84	60.71	39.29	63.26
No. 8	6/15	170°58′ E., 51°40′N	166	46.39	53.61	38.79
No. 9	7/6	171°46′ E., 49°35′N	161	29.19	70.81	09.38
No. 10	6/15	172°30′ E., 51°56′N	95	48.42	51.58	42.26
No. 11	6/5	173°38′ E., 51°38′N	73	46.58	53.42	39.11
No. 12	6/16	175°00′ E., 50°00′N	74	36.49	63.51	21.81
No. 13	8/25	175°00′ E., 51°00′N	150	72.00	28.00	82.51
No. 14	5/25	176°07′ E., 50°30′N	50	62.00	38.00	65.47
No. 15	5/28	176°04′ E., 50°22′N	87	75.86	24.14	89.16
No. 16	6/26	178°14′ E., 53°20′N	185	61.62	38.38	64.82
No. 17	8/23	180°, 51°00′N	97	64.95	35.05	70.51
No. 18	8/8	174°57′ W., 50°59′N	62	48.39	51.61	42.15
No. 19	6/20	170°02′ W., 55°59′N	297	76.43	23.57	90.12

the basis of this evidence, number of scales along the lateral line, number of vertebrae, and number of gill rakers were retained in the function utilized to classify the high-seas samples as of western Alaska or southwestern Kamchatka origin.

The lack of departure from normality as observed from examination of the individual frequency distributions for each character does not of itself ensure that the joint distribution is normal. Similarly, homogeneity of variances or slight departures thereof are not of themselves sufficient to ensure that the two covariance matrices are equal. Both factors indicate that the probability model is not rejected, but they are not sufficient of themselves to verify that the model holds; however, they provide a provisional verification that justifies the use of the discriminant function technique. This provisional verification was substantiated by the empirical test of the function in which the probabilities of misclassification for 1956 and 1957 samples of red salmon closely approximated the theoretical probabilities of misclassification (Table 17).

CLASSIFICATION OF HIGH-SEAS SAMPLES TAKEN IN 1956

The results of classifying individual red salmon as of southwestern Kamchatka or western Alaska origin for 15 samples collected on the high seas in 1956 are presented in Table 21 and Figure 6.

In the two high-seas samples taken west of longitude 165°E., 91 and 96 percent were classified as southwestern Kamchatka red salmon. Of the seven samples obtained in waters between longitudes 170°E. and 175°E., southwestern Kamchatka salmon predominated in five samples. Their predominance was most marked in sample 9 (91 percent) taken on July 6 and sample 12 (78 percent) collected on June 16. Both samples were taken on or south of latitude 50° N. The two samples predominantly of western Alaska type were sample 7 (63 percent) collected June 5 and sample 13 (82 percent) collected August 25.

With the exception of sample 18, all samples collected east of longitude 175° E. were predominantly of western Alaska type. Southwestern Kamchatka-type red salmon composed 58 percent of sample 18.

Sampling in 1956 was inadequate both as to area and as to time of sampling. Therefore only these tentative inferences are justified:

1. Preponderance of western Alaska red salmon was seen in one sample taken as far west as longitude 170°52′ E.

2. Southwestern Kamchatka-type red salmon were seen in a sample collected as far east as longitude 175° W. Red salmon in this sample were predominantly immature.

3. Marked dominance of southwestern Kamchatka red salmon was seen in two samples obtained on or

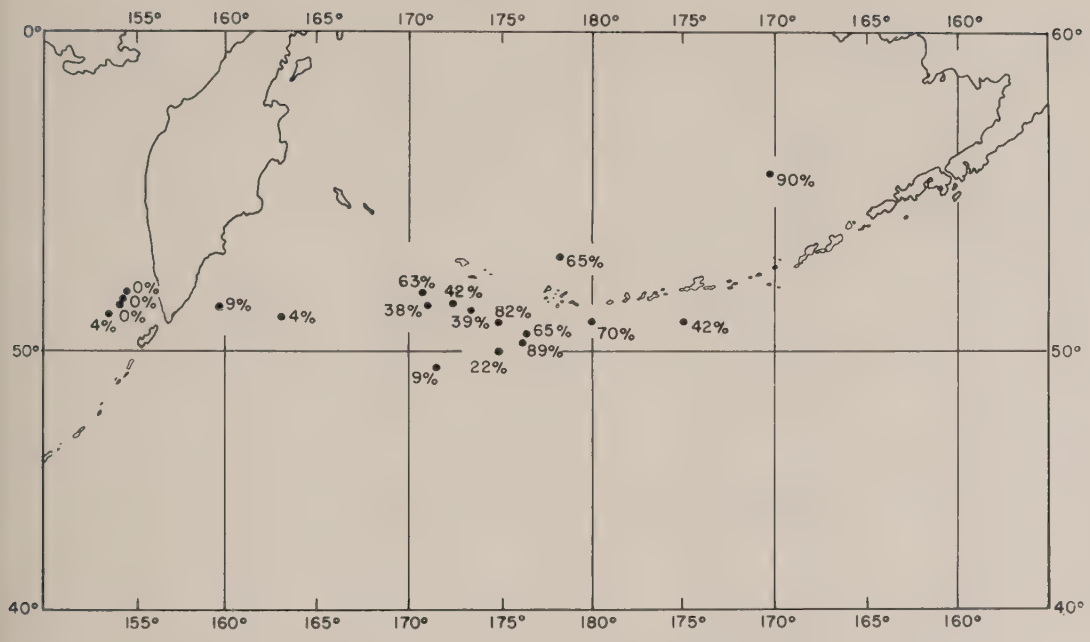

FIGURE 6. Percentage of western Alaska salmon in high-seas samples taken in 1956.

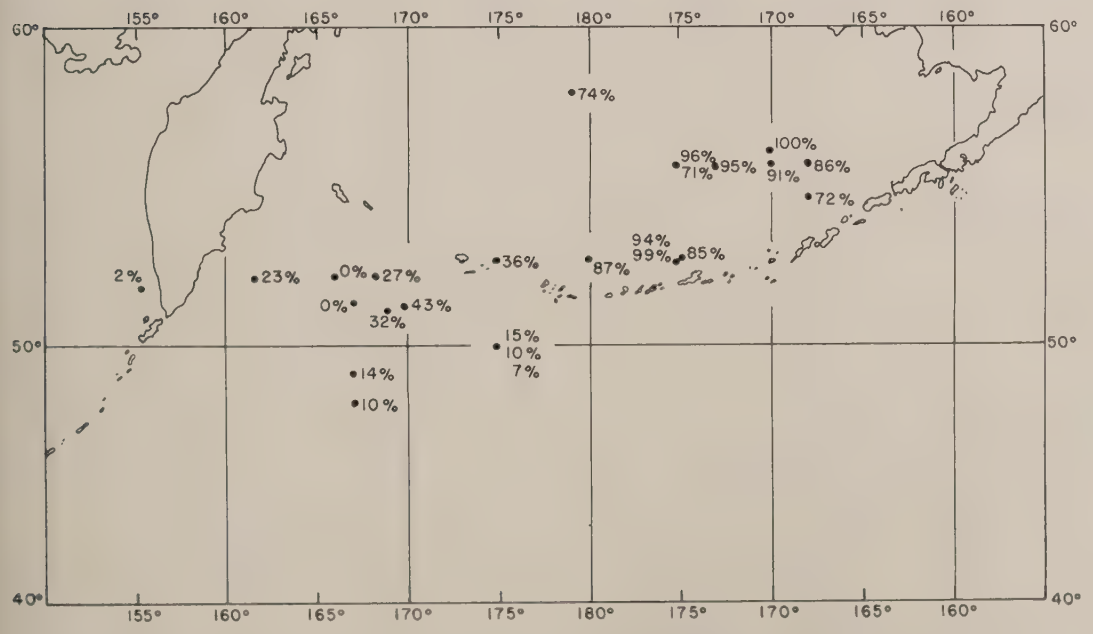

FIGURE 7. Percentage of western Alaska salmon in high-seas samples taken in May and June, 1957.

TABLE 22. Discriminant function analysis: High-seas samples of red salmon, 1957.

Sample	Sampling date	Locality	Size of sample	Percent classified — Western Alaska	Southwestern Kamchatka	Percent correct western Alaska
No. 1	7/4	153°28′ E., 50°52′N	195	25.64	74.36	03.32
No. 2	7/14	153°39′ E., 51°16′N	194	20.62	79.38	00.00
No. 3	6/24	154°15′ E., 52°08′N	192	25.00	75.00	02.22
No. 4	7/10	158°11′ E., 49°14′N	60	28.33	71.67	07.91
No. 5	7/14	158°20′ E., 49°02′N	57	29.82	70.18	10.46
No. 6	7/15	158°30′ E., 48°57′N	46	26.09	73.91	04.08
No. 7	7/24	159°45′ E., 51°31′N	89	29.21	70.79	09.42
No. 8	7/22	160°15′ E., 51°22′N	107	36.45	63.55	21.79
No. 9	6/30	161°42′ E., 52°28′N	97	37.11	62.89	22.92
No. 10	7/5	161°15′ E., 51°28′N	56	35.71	64.29	20.53
No. 11	7/10	161°21′ E., 52°36′N	114	28.95	71.05	08.97
No. 12	7/20	161°40′ E., 51°39′N	90	34.41	65.59	18.31
No. 13	7/1	162°16′ E., 51°39′N	53	22.64	77.36	00.00
No. 14	6/20	166°04′ E., 52°33′N	90	21.11	78.89	00.00
No. 15	7/15	166°48′ E., 58°12′N	56	33.93	66.07	17.59
No. 16	5/21	167°40′ E., 48°08′N	58	29.31	70.69	09.59
No. 17	5/31	167°25′ E., 49°02′N	63	31.75	68.25	13.76
No. 18	6/28	167°27′ E., 51°40′N	42	21.43	78.57	00.00
No. 19	7/13	167°27′ E., 57°26′N	30	23.33	76.67	00.00
No. 20	6/25	168°27′ E., 52°31′N	43	39.53	60.47	27.06
No. 21	5/21	169°02′ E., 51°15′N	38	42.11	57.89	31.47
No. 22	7/12	169°11′ E., 57°02′N	33	30.30	69.70	16.41
No. 23	5/27	169°55′ E., 51°28′N	39	48.72	51.28	42.77
No. 24	7/6	170°24′ E., 54°51′N	38	23.69	76.31	00.00
No. 25	6/10	175°00′ E., 50°00′N	40	32.50	67.50	15.04
No. 26	6/11	175°00′ E., 50°00′N	57	29.82	70.18	10.46
No. 27	6/12	175°00′ E., 50°00′N	54	27.78	72.22	06.80
No. 28	6/20	175°00′ E., 53°00′N	58	44.83	55.17	36.12
No. 29	8/8	175°00′ E., 50°00′N	39	51.28	48.72	47.14
No. 30	8/11	175°00′ E., 53°00′N	57	59.65	40.35	61.45
No. 31	8/12	175°00′ E., 53°00′N	83	57.83	42.17	58.34
No. 32	8/14	175°00′ E., 56°00′N	40	40.00	60.00	27.86
No. 33	8/17	175°00′ E., 53°00′N	83	63.86	36.14	68.59
No. 34	8/18	175°00′ E., 53°00′N	60	58.33	41.67	59.20
No. 35	8/19	175°00′ E., 51°30′N	144	68.75	31.25	88.87
No. 36	8/20	175°00′ E., 50°00′N	85	62.35	37.65	66.07
No. 37	8/23	175°00′ E., 51°30′N	112	62.50	37.50	66.32
No. 38	7/1	177°17′ E., 58°10′N	40	60.00	40.00	62.05
No. 39	6/27	179°10′ E., 58°15′N	58	67.24	32.76	74.42
No. 40	6/22	180°, 53°00′N	47	74.47	25.53	86.78
No. 41	7/8	176°00′ W., 51°00′N	42	76.19	23.81	89.72
No. 42	6/8	175°00′ W., 53°00′N	51	78.43	21.57	93.55
No. 43	6/9	175°03′ W., 53°01′N	53	73.58	26.42	85.26
No. 44	6/10	175°00′ W., 53°00′N	43	81.40	18.60	98.63
No. 45	6/15	175°00′ W., 56°00′N	193	79.79	20.21	95.88
No. 46	6/30	175°00′ W., 56°00′N	40	65.00	35.00	70.60
No. 47	8/6	175°03′ W., 51°30′N	45	66.67	33.33	73.45
No. 48	8/7	175°10′ W., 50°59′N	102	72.55	27.45	83.45
No. 49	8/8	175°00′ W., 49°59′N	76	60.53	39.47	62.95
No. 50	8/9	175°01′ W., 50°00′N	111	63.96	36.04	68.84
No. 51	8/20	175°01′ W., 50°00′N	46	67.39	32.61	74.68
No. 52	8/21	175°01′ W., 50°00′N	70	65.71	34.29	71.81
No. 53	8/22	175°01′ W., 50°59′N	106	72.64	27.36	83.60
No. 54	8/23	175°02′ W., 51°31′N	49	55.10	44.90	53.67
No. 55	6/17	173°00′ W., 56°00′N	148	79.05	20.95	94.60
No. 56	6/18	170°00′ W., 56°00′N	86	76.74	23.26	90.67
No. 57	6/19	170°00′ W., 56°52′N	64	87.50	12.50	100.00
No. 58	6/21	168°00′ W., 56°00′N	61	73.77	26.23	85.59
No. 59	6/22	168°00′ W., 55°00′N	85	65.88	34.12	72.00
No. 60	7/24	165°00′ W., 53°00′N	100	48.00	52.00	41.54
No. 61	7/30–31	165°00′ W., 53°00′N	46	52.17	47.83	48.67
No. 62	7/15	160°00′ W., 54°00′N	51	58.82	41.18	60.07
No. 63	7/17	160°00′ W., 52°00′N	106	42.45	57.55	32.05

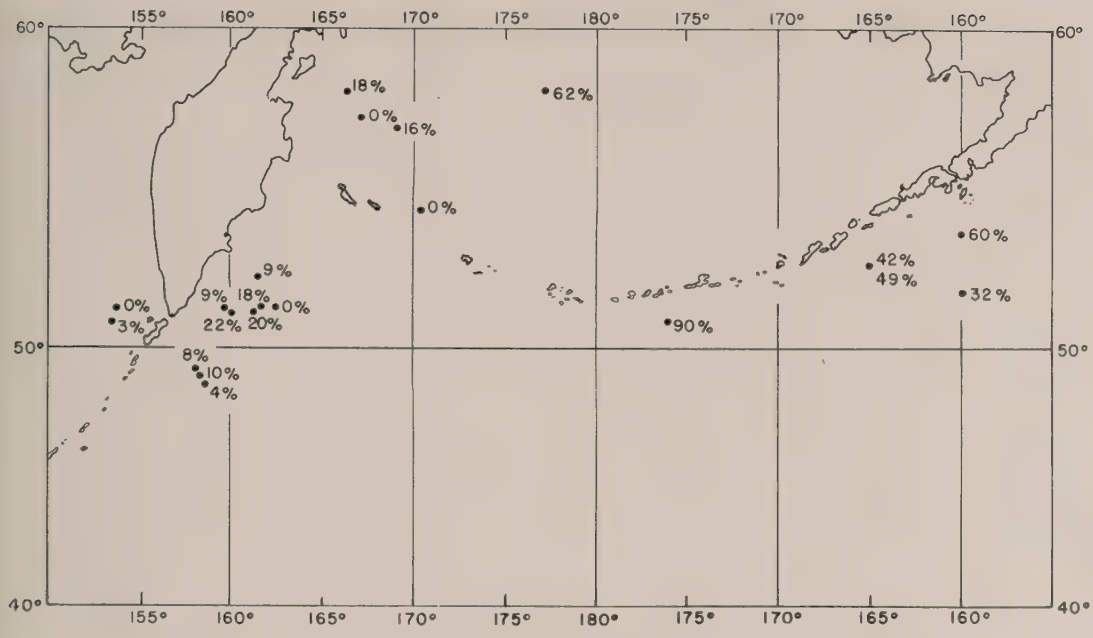

FIGURE 8. Percentage of western Alaska salmon in high-seas samples taken in July, 1957.

outh of latitude 50° N., with general southwestern Kamchatka dominance north of this latitude between ongitudes 170° E. and 174° E. in ratios of about : 4.

CLASSIFICATION OF HIGH-SEAS SAMPLES TAKEN IN 1957

Months of May and June

The results of classifying the high-seas samples aken in 1957 are shown in Table 22. The sampling areas and classification of red salmon taken in May and June are shown in Figure 7.

All samples collected west of longitude 175° E. were dominated by red salmon of southwestern Kamchatka type. However, western Alaska-type red salmon in proportions greater than 20 percent were indicated in samples 9, 20, 21, 23, and 28. With one exception (sample 9) these samples were taken east of longitude 163° E. As in 1956, in general, the percentages of western Alaska-type red salmon were lower in samples collected on or south of latitude 50° N. than north of that latitude.

East of longitude 175° E., individuals in all samples were classified predominantly as western Alaska type, ranging from 71 to 100 percent. Samples 39, 40, 43, 46, 58, and 59 were indicated to be composed of 13 to 29 percent southwestern Kamchatka-type red salmon. These samples contained mature red salmon taken from middle to late June, possibly allowing sufficient time for their return to Kamchatka. The following alternatives concerning their area of origin are considered:

1. They are, in fact, southwestern Kamchatka red salmon, as indicated by the results of classification.

2. They are elements of other North American populations, erroneously classified as from southwestern Kamchatka by virtue of the demonstrated bias in misclassification that occurs because of their comparative similarity to the southwestern Kamchatka rather than to the Bristol Bay-Kodiak-Chignik group.

3. The particular samples in question may be entirely of western Alaska origin and their misclassification as southwestern Kamchatka salmon is the result of a fault in our assumption that the samples on the high seas are distributed in proportion to their relative abundance in the streams of western Alaska. This error is clearly a possibility, for the average probability of misclassification of the western Alaska complex was reduced from 22.7 to 17.8 percent when weighted for relative abundance of the constituent populations. The Wood River population was observed to have a probability of misclassification of 40.8 percent. Therefore, if a relatively pure group of Wood River salmon were encountered on the high seas, applying the

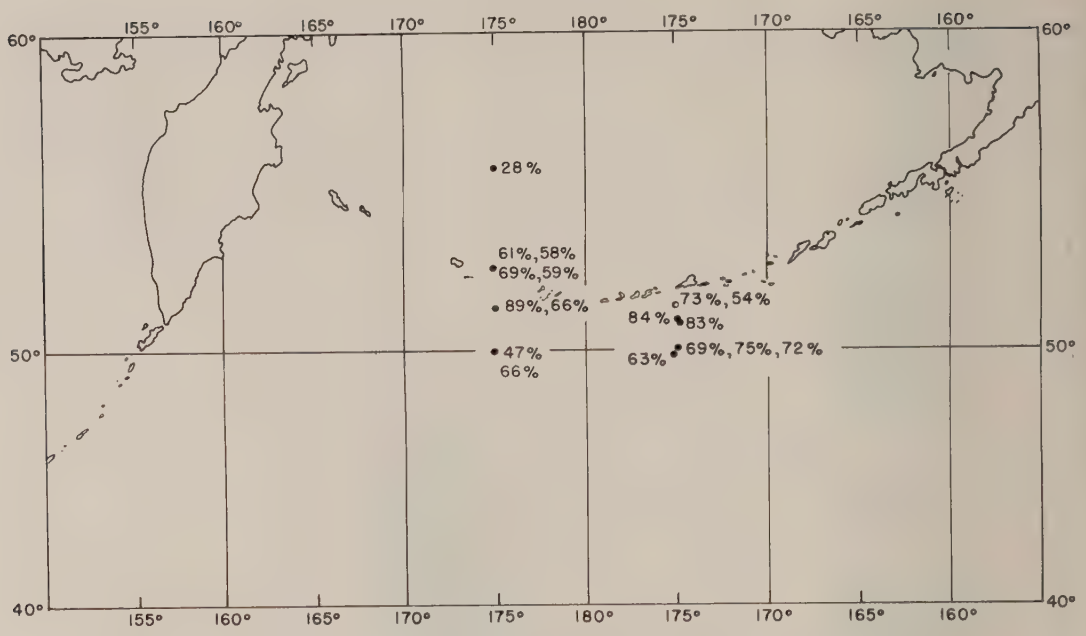

FIGURE 9. Percentage of western Alaska salmon in high-seas samples taken in August, 1957.

average weighted probability of misclassification would result in classifying some Wood River red salmon as southwestern Kamchatka fish. Results of tagging experiments conducted in these same waters lend support to this interpretation for all tagged fish returned to western Alaska with no returns from points west of the tagging sites (International North Pacific Fisheries Commission, 1958).

Month of July

Figure 8 shows the areas of sampling and results of classification for red salmon taken during the month of July.

With one exception, all samples taken west of longitude 165° W. (excluding the Okhotsk Sea sample) were obtained from the western Pacific Ocean and western Bering Sea. All samples obtained west of longitude 174°24′ E. were predominantly southwestern Kamchatka-type red salmon. In samples 8, 10, 12, 15, and 22, from 16 to 22 percent were classified as western Alaska type. Since all of these specimens were mature fish taken about the middle of July near the eastern Kamchatka coast, it is doubtful that they were actually western Alaska red salmon. Therefore, these rather large percentages of classification as western Alaska type may be the result of the following factors:

1. Misclassification may be the result of improper weighting for abundance of populations of southwestern Kamchatka. Improper weighting in this situation would be the failure to weight at all.

2. Those fish classified as from western Alaska may be from populations in Kamchatka that we have not sampled. They may be from areas other than southwestern Kamchatka or elements of the southwestern Kamchatka run which were not available to the Japanese Okhotsk Sea fishery.

The one sample collected on July 8 at 51° N., 176° W. was 90-percent western Alaska type.

Red salmon samples 60, 61, 62, and 63, collected between July 15 and July 31 at longitudes 165° W. and 160° W. were indicated to contain 58 percent, 51 percent, 40 percent, and 68 percent Asian-type salmon. If specimens in these samples taken in middle and late July were maturing, their area of origin could be presumed to be within reasonable proximity of the area of capture. However, immature fish (1 year in ocean or 2 years in ocean with immature gonads) composed the bulk of these samples. For the area from which these samples were obtained, the direct evidence on which the discriminant function analysis was based is only partially applicable. Information from tagging is lacking for this region; however, incidence of *Triaenophorus* in fish collected in samples 62 and 63 (Margolis, 1958) indicates that Bristol Bay (or Kuskokwim) salmon were present in the area

o direct evidence is available concerning the possible eas of origin of those specimens classified as from uthwestern Kamchatka. The following alternatives ould be considered concerning the possible area of igin of these specimens:

1. They are, in fact, red salmon of southwestern amchatka origin, as indicated by the results of the assification procedure, or

2. They are elements of North American popula-ons erroneously classified as from southwestern amchatka because of their relative similarity to this oup rather than to the western Alaska group.

lonth of August

All samples collected in August (Fig. 9) taken in id-ocean on or near longitudes 175° E. and 175° W. ere almost exclusively immatures. Between August and August 23, nine samples were obtained at sta-ons on or near longitude 175° E. These samples indicated considerable intermixing of western Alaska-type and southwestern Kamchatka-type salmon. Degrees of intermingling were also seen in samples 33, 35, 36, and 37, which contained 66 to 89 percent western Alaska-type red salmon.

The percentage classified as being western Alaska type ranged from 54 to 84 percent in 8 samples taken at 4 stations on or near longitude 175° W. Sample 54 in which 54 percent were classified to western Alaska was obtained at 51°31′ N. and 175° W. on August 23. At approximately the same time and location in 1956, a sample (Fig. 6, No. 18) was obtained, in which 58 percent of the sample was classified as southwestern Kamchatka. With the information at hand and with this particular function, it cannot be determined whether this sample was composed of a mixture of western Alaska and southwestern Kamchatka red salmon or a mixture of red salmon from western Alaska and other North American areas.

CONCLUSIONS

No variations were observed that were attributable differences in brood year for the seven meristic haracters used in an analysis of continental origin f red salmon taken on the high seas. Therefore, ithin the limits of the time of sampling and the areas ampled, these characters appear not to have been reatly influenced by changes in environmental condi-ons in the systems from which the samples were lected or stream conditions were not sufficiently ifferent between the years during which these speci-ens underwent embryonic development to effect lterations in morphology of the specimens examined.

Since requirements for the optimum application of he discriminant function were not entirely satisfied, he efficiency of the function as applied to red salmon eristic data was provisionally verified empirically. Comparison of the values of theoretical and empirical rror indicates that in this instance, failure to fulfill he requirements completely for optimum use of the echnique did not significantly reduce efficiency of he function.

With certain limitations, the discriminant function nalysis as applied to the problem of determining the ontinental origin of red salmon taken on the high eas yields estimates of the proportion of red salmon n each high-seas sample that originated in south-vestern Kamchatka and in western Alaska.

Results of classificatory analyses for mature red almon indicate the distribution of western Alaska red salmon in considerable proportion (greater than 30 percent per sample) as far west as longitude 168° E. Mature southwestern Kamchatka red salmon were dominant on or south of latitude 50° N. and at least as far east as longitude 175° E. However, the accuracy of these estimates must be verified by further assessment of the parameters included in our model.

The precision of the point estimate for a given sample (percentage of southwestern Kamchatka and of western Alaska red salmon) is a function of the size of the classified sample and the error of misclassification between the two reference populations. The point estimate is also subject to random-sampling variations. Therefore, the need for confidence limits for the calculated point estimates is recognized. Examination of these problems is now in progress and will be considered in subsequent analyses.

Red salmon from areas other than the two considered (southwestern Kamchatka and the Bristol Bay complex), appear to occur in particular areas. Should the problem develop into one involving more than a two-way classification, an alternative statistic should be considered for treatment of these and subsequently collected data.

Finally, the results of these and future analyses should be evaluated in the light of supplemental experimental evidence (for instance, tagging experiments).

SUMMARY

To determine the continental origin of red salmon taken on the high seas, a study of meristic characters was initiated, in which multiple characters were treated in a discriminant function analysis. Red salmon were collected from all major fishery and escapement areas in North America, from the high seas, and from waters in the proximity of the Kamchatka Peninsula. The results of these analyses are summarized.

No intra-area variation was observed to occur between sexes, fresh-water ages, ocean ages, or brood years for samples from North American streams. Therefore, the reference morphotype used in subsequent analyses was the entire sample obtained from a given stream defined by the number of scales along the lateral line, total number of vertebrae, position of the first haemal arch, number of ventral gill rakers, total number of gill rakers, number of pectoral-fin rays, and number of anal-fin elements.

Correlation of the selected meristic characters to fish length was negligible.

Samples from Bristol Bay tributaries, Kodiak Island, and Chignik River, and the Okhotsk Sea fishery were used as references in the discriminant function analysis, on the basis of supplementary biological evidence.

When samples from North American areas other than Bristol Bay, Kodiak Island, and Chignik were classified by this function, they tended to classify more often as southwestern Kamchatka rather than as western Alaska red salmon. Therefore, if red salmon from other North American areas were present in the high-seas samples, they would have been classified largely as southwestern Kamchatka fish.

Indications of intermixing of red salmon from the two continents were evident over a considerable range; the maximum westward extent of the distribution of North American red salmon occurred in the Bering Sea and the maximum eastward distribution of the southwestern Kamchatka populations occurred in the North Pacific Ocean. In general, during June a substantial percentage (greater than 70 percent per sample) of mature North American red salmon apparently occur on the high seas as far west as longitude 178°E., this percentage diminishing to 43 percent and 27 percent as far west as 168° E. Mature southwestern Kamchatka red salmon dominated the samples as far east as longitude 175° E. From lack of samples between 175° E. and 175° W., south of the Aleutians, no inference can be derived concerning the extent of the eastward distribution of southwestern Kamchatka red salmon.

The large numbers of mature red salmon in the collection of July 1957 were taken in the high-seas waters off the coast of Kamchatka. The bulk of individuals in these samples were classified as being of southwestern Kamchatka origin (70–100 percent).

The area of origin of the immature specimens taken in July and August can be asserted with some degree of confidence only for those portions classified into the Bristol Bay complex. The remaining specimens may be from Asian or North American areas other than those used in the North American standard.

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APPENDICES

APPENDIX A. CUMULATIVE ESCAPEMENTS IN WESTERN ALASKA STREAMS, 1956 AND 1957.

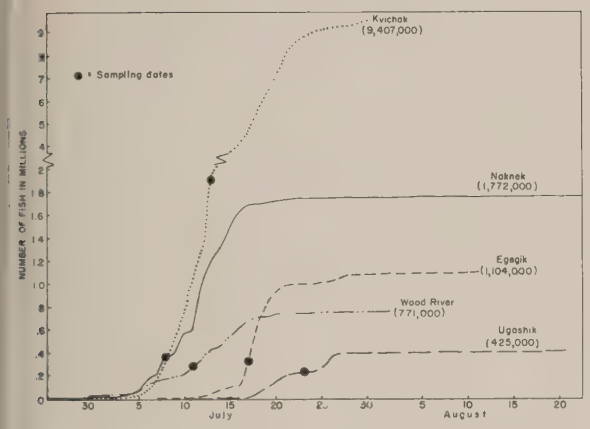

FIGURE A–1. Cumulative escapements of red salmon in Bristol Bay streams, 1956.

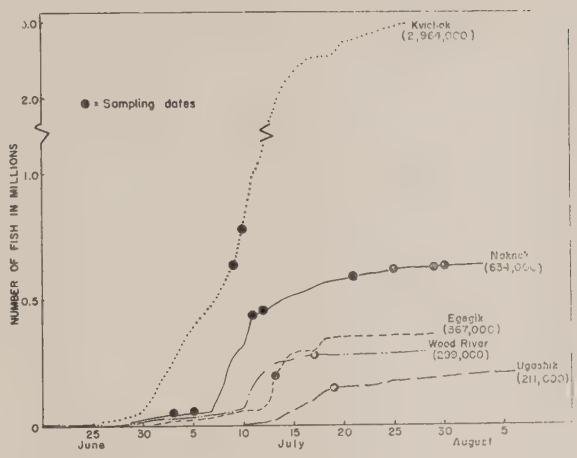

FIGURE A–2. Cumulative escapements of red salmon in Bristol Bay streams, 1957.

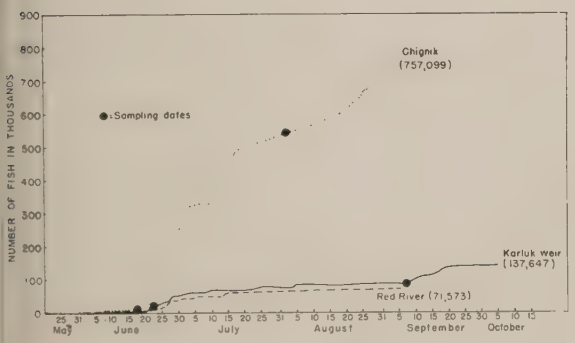

FIGURE A–3. Cumulative escapements of red salmon in Karluk weir, Chignik, 1956.

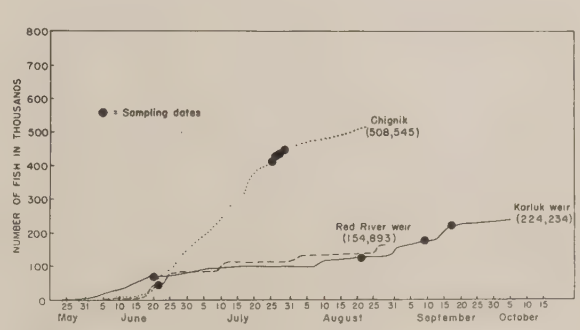

FIGURE A–4. Cumulative escapements of red salmon in Karluk weir, Chignik, 1957.

APPENDIX B. INTRA-AREA SOURCES OF VARIATIONS FOR TEN MERISTIC CHARACTERS

Tables B–1 to B–10. Sexual dimorphism in ten meristic characters in red salmon collected in 1956.

Tables B–11 to B–20. Sexual dimorphism in ten meristic characters in red salmon collected in 1957.

Tables B–21 to B–30. Effect of fresh-water age on ten meristic characters in red salmon collected in 1955–57.

Tables B–31 to B–40. Effect of ocean age on ten meristic characters in red salmon collected in 1955–57.

Tables B–41 to B–50. Effect of brood year on ten meristic characters in red salmon collected in 1955–57.

Tables B–51 to B–60. Effect of time of sampling on ten meristic characters in red salmon collected in 1955–57.

TABLE B–1. Sexual dimorphism in number of scales along the lateral line in red salmon collected in 1956.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Bonneville Dam	7/2	4_2	M	17	126.353	3.743	0.469	0.776	0.392
			F	16	127.000	5.200	0.570		
McNary	7/12	4_2	M	20	127.350	4.026	0.448	2.949	0.086
			F	18	128.389	2.841	0.389		
Adak Island:									
Kagalaska	7/24	6_3	M	21	124.762	4.490	0.154	0.007	0.950
			F	22	129.818	5.014	0.477		
Do	7/31	6_3	M	24	129.375	2.765	0.339	0.004	0.860
			F	15	129.267	3.921	0.501		
Kodiak Island:									
Karluk weir	9/7	6_4	M	34	130.647	4.479	0.362	0.365	0.550
			F	34	130.941	3.573	0.324		
Do	6/22	6_4	M	36	130.056	3.714	0.311	0.899	0.350
			F	19	129.579	2.033	0.327		
Do	6/22	7_4	M	16	130.750	3.400	0.451	0.006	0.960
			F	31	130.710	2.413	0.278		
Bristol Bay:									
Naknek weir	7/8	5_2	M	16	130.313	7.293	0.675	0.153	0.695
			F	18	130.611	2.841	0.397		
Do	7/8	6_3	M	14	129.357	5.785	0.642	0.954	0.344
			F	25	130.200	7.167	0.535		
Egegik weir	7/17	5_3	M	69	130.043	2.337	0.183	0.088	0.770
			F	41	129.951	2.748	0.258		
Ugashik weir	7/23	4_2	M	65	130.231	3.398	0.228	0.008	0.955
			F	58	130.259	2.475	0.206		
Do	7/23	5_3	M	16	129.813	3.227	0.449	0.036	0.850
			F	19	129.684	4.561	0.489		
Kvichak River	7/13	4_2	M	53	130.962	3.498	0.256	0.514	0.475
			F	55	130.673	5.261	0.309		
Do	7/13	5_3	M	30	131.600	4.731	0.397	0.088	0.770
			F	23	131.435	3.077	0.365		
Wood River	7/11	4_2	M	43	129.860	3.790	0.296	0.0002	0.980
			F	75	129.867	3.415	0.213		
Cook Inlet:									
Fish Creek	7/25	4_2	M	16	126.188	5.493	0.585	[1]4.542	0.042
			F	14	127.714	1.915	0.369		

[1] Significant at 5-percent level.

TABLE B–2. Sexual dimorphism in number of scales below the lateral line in red salmon collected in 1956.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Bonneville Dam	7/2	4_2	M	17	20.118	1.365	0.283	0.015	0.905
			F	16	20.063	1.926	0.142		
McNary	7/12	4_2	M	20	19.950	1.205	0.245	0.218	0.639
			F	18	20.111	1.047	0.241		
Adak Island:									
Kagalaska	7/24	6_3	M	21	19.762	0.890	0.205	0.140	0.705
			F	22	19.864	0.695	0.177		
Do	7/31	6_3	M	24	19.792	0.782	0.180	0.037	0.845
			F	15	19.733	0.921	0.247		
Kodiak Island:									
Karluk weir	9/7	6_4	M	34	19.647	1.084	0.178	0.170	0.675
			F	35	19.743	0.785	0.149		
Do	6/22	6_4	M	36	19.694	1.245	0.186	0.017	0.890
			F	19	19.737	1.427	0.274		
Do	6/22	7_4	M	16	20.188	0.960	0.244	1.530	0.223
			F	31	20.581	1.116	0.189		
Bristol Bay:									
Naknek weir	7/8	5_2	M	16	19.875	1.846	0.339	0.002	0.975
			F	18	19.889	0.694	0.196		
Do	7/8	6_3	M	14	20.214	1.107	0.281	0.951	0.350
			F	25	19.880	1.025	0.202		
Egegik weir	7/17	5_3	M	69	20.145	1.244	0.134	3.721	0.055
			F	42	19.762	0.673	0.126		
Ugashik weir	7/23	4_2	M	65	19.785	1.078	0.128	0.652	0.423
			F	58	19.638	0.936	0.126		
Do	7/23	5_3	M	16	19.125	1.180	0.271	0.445	0.507
			F	19	19.368	1.133	0.244		
Kvichak River	7/13	4_2	M	53	21.038	1.267	0.154	0.148	0.690
			F	56	20.964	0.725	0.113		
Do	7/13	5_3	M	30	20.467	1.569	0.228	0.333	0.567
			F	23	20.652	1.054	0.214		
Wood River	7/11	4_2	M	43	20.488	0.826	0.138	2.131	0.148
			F	75	20.227	0.906	0.109		
Cook Inlet:									
Fish Creek	7/25	4_2	M	16	20.813	1.760	0.331	1.555	0.222
			F	14	20.286	0.838	0.399		

TABLE B–3. Sexual dimorphism in number of vertebrae in red salmon collected in 1956.

Area	Date	Age group	Sex	*N*	Mean	Variance	Standard error	*F*-value	*P*
Columbia River:									
Bonneville Dam	7/2	4_2	M	17	66.47	1.012	0.243	0.201	0.645
			F	16	66.31	1.026	0.253		
McNary	7/12	4_2	M	22	66.36	0.719	0.180	1.188	0.340
			F	18	66.67	0.823	0.213		
Adak Island:									
Kagalaska	7/24	6_3	M	21	67.10	0.890	0.205	0.021	0.880
			F	22	67.14	0.790	0.189		
Do	7/31	6_3	M	24	66.92	0.773	0.179	1.828	0.183
			F	16	67.31	0.893	0.236		
Kodiak Island:									
Karluk weir	9/7	6_4	M	34	67.56	0.800	0.187	3.273	0.075
			F	33	67.18	0.653	0.140		
Do	6/22	6_4	M	36	66.89	0.845	0.153	0.000	0.999
			F	19	66.90	0.322	0.130		
Do	6/22	7_4	M	16	67.31	0.493	0.175	0.459	0.500
			F	31	67.16	0.540	0.131		
Bristol Bay:									
Naknek weir	7/8	5_2	M	16	67.44	1.460	0.302	0.087	0.770
			F	18	67.34	0.705	0.198		
Do	7/8	6_3	M	14	67.21	0.492	0.187	0.666	0.423
			F	25	67.52	1.675	0.258		
Egegik weir	7/17	5_3	M	69	67.26	0.577	0.091	0.242	0.620
			F	42	67.19	0.451	0.103		
Ugashik weir	7/23	4_2	M	64	67.31	0.407	0.079	0.420	0.529
			F	55	67.24	0.405	0.085		
Do	7/23	5_3	M	15	67.13	0.692	0.214	0.734	0.402
			F	19	67.37	0.577	0.174		
Kvichak River	7/13	4_2	M	54	67.44	0.552	0.101	0.805	0.376
			F	56	67.30	0.796	0.119		
Do	7/13	5_3	M	28	67.68	1.188	0.205	0.330	0.566
			F	23	67.52	0.622	0.164		
Wood River	7/11	4_2	M	43	67.14	0.504	0.108	1.488	0.225
			F	75	67.32	0.652	0.093		
Cook Inlet:									
Fish Creek	7/25	4_2	M	16	65.44	1.060	0.257	3.964	0.054
			F	15	66.00	0.142	0.097		

TABLE B–4. Sexual dimorphism in position of first haemal arch in red salmon collected in 1956.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Bonneville Dam	7/2	4_2	M	17	34.29	0.968	0.238	4.097	0.051
			F	16	33.69	0.493	0.175		
McNary	7/12	4_2	M	22	33.91	0.752	0.184	1.477	0.232
			F	18	34.22	0.535	0.172		
Adak Island:									
Kagalaska	7/24	6_3	M	21	34.29	0.815	0.197	0.882	0.357
			F	22	34.54	0.833	0.194		
Do	7/31	6_3	M	24	34.21	0.434	0.134	0.127	0.720
			F	16	34.12	0.646	0.201		
Kodiak Island:									
Karluk weir	9/7	6_4	M	34	34.71	1.124	0.181	3.398	0.074
			F	33	34.30	0.468	0.119		
Do	6/22	6_4	M	36	34.58	0.534	0.121	0.079	0.780
			F	19	34.53	0.483	0.159		
Do	6/22	7_4	M	16	34.50	0.266	0.128	0.044	0.830
			F	31	34.45	0.723	0.152		
Bristol Bay:									
Naknek weir	7/8	5_2	M	16	34.81	0.426	0.163	1.969	0.169
			F	18	34.39	1.076	0.244		
Do	7/8	6_3	M	14	34.50	0.576	0.203	0.075	0.780
			F	24	34.41	0.947	0.198		
Egegik weir	7/17	5_3	M	69	34.58	0.482	0.083	0.058	0.803
			F	42	34.55	0.448	0.103		
Ugashik weir	7/23	4_2	M	64	34.52	0.476	0.086	1.182	0.278
			F	55	34.66	0.488	0.093		
Do	7/23	5_3	M	15	34.53	0.550	0.191	0.913	0.351
			F	19	34.26	0.761	0.200		
Kvichak River	7/13	4_2	M	54	34.78	1.081	0.141	0.565	0.457
			F	57	34.65	0.553	0.098		
Do	7/13	5_3	M	28	34.93	0.737	0.162	0.389	0.535
			F	23	34.78	0.631	0.165		
Wood River	7/11	4_2	M	43	34.46	0.635	0.121	1.750	0.186
			F	75	34.27	0.604	0.089		
Cook Inlet:									
Fish Creek	7/25	4_2	M	16	33.06	1.393	0.295	2.142	0.156
			F	15	33.67	1.235	0.286		

TABLE B–5. Sexual dimorphism in number of ventral gill rakers in red salmon collected in 1956.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Bonneville Dam	7/2	4_2	M	15	21.667	1.378	0.303	0.934	0.345
			F	14	22.071	1.146	0.286		
McNary	7/12	4_2	M	22	21.818	0.919	0.204	0.013	0.925
			F	18	21.778	1.476	0.286		
Adak Island:									
Kagalaska	7/24	6_3	M	21	21.048	0.850	0.201	0.246	0.617
			F	22	21.182	0.728	0.181		
Do	7/31	6_3	M	24	21.375	0.765	0.178	[1]4.434	0.041
			F	16	20.813	0.560	0.187		
Kodiak Island:									
Karluk weir	9/7	6_4	M	34	22.676	0.769	0.150	0.331	0.564
			F	35	22.543	1.079	0.175		
Do	6/22	6_4	M	36	22.444	0.540	0.122	1.203	0.275
			F	19	22.211	0.622	0.180		
Do	6/22	7_4	M	16	23.000	1.333	0.288	1.389	0.244
			F	31	22.645	0.770	0.157		
Bristol Bay:									
Naknek weir	7/8	5_2	M	16	23.063	0.593	0.192	0.050	0.820
			F	18	23.000	0.705	0.198		
Do	7/8	6_3	M	14	23.000	0.769	0.234	0.014	0.912
			F	25	23.040	1.291	0.227		
Egegik weir	7/17	5_3	M	68	23.132	0.743	0.104	1.522	0.222
			F	42	22.905	1.112	0.162		
Ugashik weir	7/23	4_2	M	64	22.938	0.820	0.113	0.131	0.715
			F	55	23.000	0.963	0.132		
Do	7/23	5_3	M	15	22.800	0.742	0.222	0.048	0.835
			F	19	22.737	0.650	0.184		
Kvichak River	7/13	4_2	M	54	23.056	0.769	0.119	0.269	0.604
			F	56	23.143	0.780	0.117		
Do	7/13	5_3	M	29	23.034	0.892	0.175	0.040	0.845
			F	23	23.087	0.809	0.187		
Wood River	7/11	4_2	M	43	22.744	0.671	0.124	1.070	0.304
			F	75	22.573	0.787	0.102		
Cook Inlet:									
Fish Creek	7/25	4_2	M	16	21.813	1.093	0.261	0.171	0.675
			F	15	21.667	0.807	0.231		

[1] Significant at 5-percent level.

TABLE B–6. Sexual dimorphism in number of gill rakers in red salmon collected in 1956.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Bonneville Dam	7/2	4_2	M	15	35.200	2.171	0.370	0.420	0.519
			F	14	35.500	0.884	0.251		
McNary	7/12	4_2	M	22	35.091	2.657	0.347	0.098	0.755
			F	18	35.278	4.564	0.503		
Adak Island:									
Kagalaska	7/24	6_3	M	21	34.095	1.390	0.257	0.054	0.815
			F	22	34.182	1.585	0.268		
Do	7/31	6_3	M	24	34.375	1.200	0.223	3.829	0.057
			F	16	33.688	1.160	0.269		
Kodiak Island:									
Karluk weir	9/7	6_4	M	33	36.545	1.568	0.217	0.567	0.457
			F	35	36.286	2.444	0.264		
Do	6/22	6_4	M	34	36.353	1.145	0.183	1.877	0.173
			F	19	35.895	1.766	0.304		
Do	6/22	7_4	M	16	36.750	2.600	0.403	0.095	0.755
			F	31	36.613	1.846	0.243		
Bristol Bay:									
Naknek weir	7/8	5_2	M	16	37.188	1.360	0.291	0.046	0.830
			F	18	37.111	0.811	0.212		
Do	7/8	6_3	M	14	37.214	2.953	0.459	0.002	0.886
			F	25	37.240	2.358	0.307		
Egegik weir	7/17	5_3	M	68	37.338	1.838	0.164	0.131	0.718
			F	42	37.238	2.185	0.228		
Ugashik weir	7/23	4_2	M	64	37.141	1.804	0.167	0.075	0.790
			F	55	37.073	1.772	0.179		
Do	7/23	5_3	M	15	36.933	2.207	0.383	0.441	0.512
			F	19	36.632	1.355	0.267		
Kvichak River	7/13	4_2	M	54	37.426	1.456	0.164	0.092	0.762
			F	56	37.357	1.361	0.155		
Do	7/13	5_3	M	29	37.276	2.064	0.266	0.162	0.685
			F	23	37.435	1.895	0.287		
Wood River	7/11	4_2	M	43	36.674	1.700	0.198	1.118	0.292
			F	75	36.400	1.918	0.159		
Cook Inlet:									
Fish Creek	7/25	4_2	M	16	35.063	2.460	0.382	0.133	0.718
			F	15	34.867	1.978	0.363		

TABLE B–7. Sexual dimorphism in number of branchiostegal rays in red salmon collected in 1956.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Bonneville Dam	7/2	4_2	M	16	13.438	0.260	0.127	3.258	0.080
			F	16	13.813	0.426	0.163		
McNary	7/12	4_2	M	22	13.545	0.547	0.157	0.000	0.999
			F	18	13.556	0.494	0.165		
Adak Island:									
Kagalaska	7/24	6_3	M	21	13.762	0.590	0.167	0.084	0.770
			F	20	13.700	0.326	0.127		
Do	7/31	6_3	M	24	13.667	0.491	0.142	2.203	0.145
			F	16	13.313	0.626	0.197		
Kodiak Island:									
Karluk weir	9/7	6_4	M	33	13.636	0.550	0.128	0.012	0.920
			F	35	13.657	0.585	0.129		
Do	6/22	6_4	M	36	13.444	0.654	0.134	0.013	0.915
			F	19	13.421	0.255	0.115		
Do	6/22	7_4	M	16	13.750	0.333	0.144	1.749	0.191
			F	31	14.065	0.730	0.153		
Bristol Bay:									
Naknek weir	7/8	5_2	M	15	13.400	0.400	0.163	0.049	0.820
			F	18	13.444	0.258	0.119		
Do	7/8	6_3	M	14	13.784	0.338	0.155	1.870	0.177
			F	25	13.480	0.508	0.142		
Egegik weir	7/17	5_3	M	69	13.754	0.423	0.078	0.013	0.925
			F	42	13.738	0.343	0.090		
Ugashik weir	7/23	4_2	M	65	13.892	0.346	0.072	0.002	0.980
			F	53	13.887	0.371	0.083		
Do	7/23	5_3	M	14	13.714	0.838	0.245	0.000	0.999
			F	18	13.722	0.211	0.108		
Kvichak River	7/13	4_2	M	54	13.778	0.628	0.107	0.026	0.870
			F	57	13.754	0.439	0.086		
Do	7/13	5_3	M	28	13.750	0.340	0.110	0.224	0.635
			F	23	13.652	0.781	0.184		
Wood River	7/11	4_2	M	43	13.651	0.519	0.109	0.351	0.552
			F	74	13.568	0.550	0.086		
Cook Inlet:									
Fish Creek	7/25	4_2	M	16	12.813	0.826	0.227	[1]5.291	0.032
			F	15	13.467	0.407	0.164		

[1] Significant at 5-percent level.

TABLE B–8. Sexual dimorphism in number of pectoral-fin rays in red salmon collected in 1956.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Bonneville Dam	7/2	4_2	M	17	15.176	0.156	0.095	[1]6.746	0.014
			F	16	15.688	0.493	0.175		
McNary	7/12	4_2	M	22	15.591	0.347	0.125	0.008	0.940
			F	18	15.611	0.370	0.143		
Adak Island:									
Kagalaska	7/24	6_3	M	21	15.857	0.230	0.104	0.067	0.795
			F	22	15.818	0.252	0.106		
Do	7/31	6_3	M	24	15.708	0.391	0.127	0.318	0.572
			F	15	15.600	0.257	0.130		
Kodiak Island:									
Karluk weir	9/7	6_4	M	34	16.706	0.336	0.099	[1]4.258	0.042
			F	35	16.400	0.423	0.110		
Do	6/22	6_4	M	36	16.528	0.257	0.084	0.425	0.517
			F	19	16.421	0.477	0.158		
Do	6/22	7_4	M	16	16.375	0.513	0.178	0.005	0.965
			F	31	16.387	0.313	0.100		
Bristol Bay:									
Naknek weir	7/8	5_2	M	16	16.000	0.400	0.158	3.991	0.054
			F	18	16.389	0.252	0.118		
Do	7/8	6_3	M	14	16.429	0.415	0.172	0.339	0.562
			F	24	16.250	1.065	0.210		
Egegik weir	7/17	5_3	M	69	16.551	0.310	0.066	2.490	0.117
			F	42	16.381	0.290	0.083		
Ugashik weir	7/23	4_2	M	65	16.508	0.253	0.061	0.130	0.717
			F	55	16.473	0.290	0.072		
Do	7/23	5_3	M	15	16.333	0.235	0.125	2.036	0.165
			F	19	16.579	0.255	0.115		
Kvichak River	7/13	4_2	M	54	16.611	0.354	0.080	2.221	0.140
			F	56	16.429	0.467	0.091		
Do	7/13	5_3	M	29	16.379	0.385	0.115	0.038	0.855
			F	23	16.348	0.236	0.101		
Wood River	7/11	4_2	M	43	16.419	0.297	0.083	1.244	0.267
			F	75	16.293	0.371	0.070		
Cook Inlet:									
Fish Creek	7/25	4_2	M	15	15.867	0.264	0.132	0.482	0.489
			F	15	16.000	0.285	0.137		

[1] Significant at 5-percent level.

TABLE B–9. Sexual dimorphism in number of dorsal-fin elements in red salmon collected in 1956.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Bonneville Dam	7/2	4_2	M	17	14.176	0.406	0.154	0.291	0.591
			F	16	14.063	0.326	0.142		
McNary	7/12	4_2	M	22	14.091	0.371	0.129	0.039	0.840
			F	18	14.056	0.170	0.097		
Adak Island:									
Kagalaska	7/24	6_3	M	21	14.000	0.400	0.137	0.228	0.630
			F	22	14.091	0.370	0.129		
Do	7/31	6_3	M	24	14.208	0.521	0.147	0.127	0.720
			F	16	14.125	0.513	0.178		
Kodiak Island:									
Karluk weir	9/7	6_4	M	33	14.636	0.362	0.104	0.017	0.895
			F	35	14.647	0.467	0.115		
Do	6/22	6_4	M	36	14.694	0.445	0.110	0.055	0.810
			F	19	14.737	0.316	0.128		
Do	6/22	7_4	M	16	14.500	0.400	0.158	0.007	0.955
			F	31	14.516	0.456	0.121		
Bristol Bay:									
Naknek weir	7/8	5_2	M	16	14.563	0.526	0.181	0.000	0.999
			F	18	14.556	0.376	0.144		
Do	7/8	6_3	M	14	14.429	0.261	0.136	0.633	0.434
			F	25	14.600	0.500	0.141		
Egegik weir	7/17	5_3	M	69	14.667	0.313	0.067	0.186	0.662
			F	42	14.714	0.307	0.085		
Ugashik weir	7/23	4_2	M	64	14.453	0.347	0.073	0.580	0.452
			F	54	14.537	0.366	0.081		
Do	7/23	5_3	M	15	14.867	0.264	0.132	3.957	0.055
			F	19	14.474	0.372	0.139		
Kvichak River	7/13	4_2	M	53	14.943	0.361	0.082	[1]6.591	0.011
			F	56	14.661	0.301	0.072		
Do	7/13	5_3	M	29	14.517	0.400	0.117	0.283	0.594
			F	23	14.609	0.340	0.121		
Wood River	7/11	4_2	M	42	14.667	0.422	0.100	0.516	0.476
			F	74	14.581	0.356	0.069		
Cook Inlet:									
Fish Creek	7/25	4_2	M	16	14.188	0.160	0.100	1.264	0.270
			F	15	14.400	0.400	0.163		

[1] Significant at 5-percent level.

TABLE B–10. Sexual dimorphism in number of anal-fin elements in red salmon collected in 1956.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Bonneville Dam	7/2	4_2	M	17	17.412	0.256	0.122	1.482	0.232
			F	16	17.625	0.246	0.124		
McNary	7/12	4_2	M	22	17.500	0.642	0.170	0.000	0.999
			F	18	17.500	0.264	0.121		
Adak Island:									
Kagalaska	7/24	6_3	M	21	16.952	0.350	0.128	0.090	0.765
			F	22	17.000	0.190	0.092		
Do	7/31	6_3	M	24	17.042	0.565	0.153	0.246	0.618
			F	16	16.938	0.193	0.109		
Kodiak Island:									
Karluk weir	9/7	6_4	M	34	18.029	0.212	0.078	0.059	0.801
			F	35	18.000	0.294	0.091		
Do	6/22	6_4	M	36	17.889	0.388	0.103	0.109	0.667
			F	19	17.947	0.383	0.141		
Do	6/22	7_4	M	16	18.000	0.400	0.158	[1]4.639	0.036
			F	31	17.613	0.313	0.100		
Bristol Bay:									
Naknek weir	7/8	5_2	M	16	18.000	0.266	0.128	0.000	0.999
			F	18	18.000	0.235	0.114		
Do	7/8	6_3	M	14	18.000	0.307	0.148	0.108	0.740
			F	25	17.920	0.658	0.162		
Egegik weir	7/17	5_3	M	68	17.926	0.337	0.700	0.140	0.720
			F	42	17.881	0.448	0.103		
Ugashik weir	7/23	4_2	M	65	17.892	0.159	0.049	0.129	0.717
			F	54	17.926	0.371	0.082		
Do	7/23	5_3	M	15	18.067	0.350	0.152	[1]4.344	0.048
			F	19	17.684	0.227	0.109		
Kvichak River	7/13	4_2	M	53	17.830	0.375	0.083	0.242	0.621
			F	56	17.893	0.498	0.093		
Do	7/13	5_3	M	26	17.962	0.360	0.117	0.078	0.775
			F	23	17.913	0.354	0.124		
Wood River	7/11	4_2	M	43	17.953	0.426	0.099	0.433	0.512
			F	74	18.041	0.505	0.082		
Cook Inlet:									
Fish Creek	7/25	4_2	M	15	17.667	0.521	0.186	0.757	0.395
			F	15	17.467	0.264	0.132		

[1] Significant at 5-percent level.

TABLE B–11. Sexual dimorphism in number of scales along the lateral line in red salmon collected in 1957.

Area	Date	Age group	Sex	*N*	Mean	Variance	Standard error	*F*-value	*P*
Columbia River:									
Tumwater	8/12	4_2	M	16	126.875	7.713	0.694	0.974	0.334
			F	18	127.778	6.535	0.602		
Kodiak Island:									
Karluk weir	9/17	5_3	M	21	129.952	4.750	0.475	0.068	0.792
			F	18	129.778	3.829	0.461		
Red River	6/21	5_2	M	28	131.036	1.444	0.227	0.000	0.999
			F	25	131.040	2.958	0.343		
Do	6/21	5_3	M	37	130.459	2.088	0.237	1.662	0.202
			F	21	131.048	4.050	0.439		
Do	6/21	6_3	M	24	130.917	2.600	0.329	0.879	0.357
			F	22	131.318	1.561	0.266		
Bristol Bay:									
Naknek weir	7/3	6_3	M	17	131.118	2.112	0.352	0.020	0.885
			F	28	131.036	4.407	0.396		
Do	7/5	5_2	M	15	129.600	3.257	0.465	0.188	0.660
			F	15	129.867	2.407	0.400		
Do	7/5	6_3	M	29	130.828	5.646	0.441	1.657	0.202
			F	33	130.212	1.671	0.225		
Do	7/11	6_3	M	18	130.111	3.047	0.411	1.041	0.316
			F	17	130.647	1.743	0.320		
Do	7/12	6_3	M	24	131.042	6.565	0.523	0.422	0.517
			F	24	131.500	5.391	0.473		
Do	7/21	6_3	M	19	131.000	6.888	0.602	0.340	0.561
			F	20	130.550	4.784	0.489		
Do	7/25	6_3	M	30	130.733	5.858	0.441	1.216	0.275
			F	45	131.356	5.643	0.354		
Egegik weir	7/13	6_3	M	49	130.653	3.939	0.283	1.622	0.205
			F	57	130.140	4.551	0.282		
Ugashik weir	7/19	5_2	M	26	130.615	1.848	0.266	0.188	0.660
			F	41	130.463	2.005	0.221		
Kvichak River	7/9	5_2	M	21	130.429	2.755	0.362	[1]4.503	0.038
			F	32	131.375	2.371	0.272		
Do	7/10	5_2	M	23	130.348	2.781	0.347	3.196	0.081
			F	25	131.200	2.666	0.326		
Wood River	7/17	5_2	M	23	129.609	2.613	0.337	0.038	0.840
			F	22	129.500	4.357	0.445		

[1] Significant at 5-percent level.

TABLE B–12. Sexual dimorphism in number of scales below the lateral line in red salmon collected in 1957.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Tumwater	8/12	4_2	M	16	19.750	1.000	0.250	0.894	0.356
			F	18	20.000	0.235	0.114		
Kodiak Island:									
Karluk weir	9/17	5_3	M	20	20.350	1.500	0.273	3.916	0.053
			F	18	19.556	1.552	0.293		
Red River	6/21	5_2	M	28	20.964	0.925	0.181	0.193	0.658
			F	25	21.080	0.908	0.190		
Do	6/21	5_3	M	37	20.811	0.880	0.154	1.126	0.293
			F	21	20.524	1.160	0.235		
Do	6/21	6_3	M	24	20.417	1.295	0.232	3.932	0.051
			F	22	21.045	1.000	0.213		
Bristol Bay:									
Naknek weir	7/3	6_3	M	17	19.471	0.887	0.228	[1]4.128	0.050
			F	28	20.036	0.777	0.166		
Do	7/5	5_2	M	15	20.267	0.635	0.205	0.163	0.687
			F	15	20.133	0.978	0.255		
Do	7/5	6_3	M	29	20.000	0.857	0.171	1.046	0.312
			F	33	19.758	0.878	0.163		
Do	7/11	6_3	M	18	19.278	0.917	0.225	3.590	0.066
			F	17	19.882	0.862	0.225		
Do	7/12	6_3	M	24	19.625	0.852	0.188	0.857	0.363
			F	24	19.875	0.895	0.193		
Do	7/21	6_3	M	19	19.842	0.694	0.191	0.867	0.362
			F	20	19.550	1.205	0.245		
Do	7/25	6_3	M	30	19.800	0.717	0.154	0.084	0.765
			F	45	19.733	1.109	0.157		
Egegik weir	7/13	6_3	M	49	19.878	0.818	0.129	0.008	0.950
			F	57	19.860	0.944	0.128		
Ugashik weir	7/19	5_2	M	26	19.385	0.408	0.125	[1]4.998	0.028
			F	41	19.805	0.660	0.126		
Kvichak River	7/9	5_2	M	21	20.429	0.855	0.201	3.663	0.058
			F	32	21.031	1.516	0.217		
Do	7/10	5_2	M	23	20.652	0.781	0.184	0.011	0.915
			F	25	20.680	0.808	0.179		
Wood River	7/17	5_2	M	23	20.348	1.054	0.214	0.128	0.719
			F	22	20.455	0.928	0.205		

[1] Significant at 5-percent level.

TABLE B–13. Sexual dimorphism in number of vertebrae in red salmon collected in 1957.

Area	Date	Age group	Sex	*N*	Mean	Variance	Standard error	*F*-value	*P*
Columbia River:									
Tumwater	8/12	4_2	M	16	65.813	1.093	0.261	2.636	0.116
			F	17	66.353	0.743	0.209		
Kodiak Island:									
Karluk weir	9/17	5_3	M	21	67.238	0.490	0.152	0.137	0.710
			F	18	57.333	0.823	0.213		
Red River	6/21	5_2	M	28	67.464	0.703	0.158	0.779	0.385
			F	25	67.640	0.325	0.114		
Do	6/21	5_3	M	36	67.306	0.388	0.103	1.275	0.263
			F	20	67.550	0.994	0.223		
Do	6/21	6_3	M	24	67.458	0.608	0.159	0.177	0.674
			F	22	67.545	0.357	0.127		
Bristol Bay:									
Naknek weir	7/3	6_3	M	17	67.706	0.843	0.222	0.558	0.462
			F	26	67.500	0.740	0.168		
Do	7/5	5_2	M	14	66.929	0.684	0.221	0.055	0.815
			F	14	66.857	0.592	0.205		
Do	7/5	6_3	M	28	67.571	0.996	0.188	[1]5.870	0.018
			F	31	67.065	0.330	0.103		
Do	7/11	6_3	M	17	67.294	0.718	0.205	0.040	0.840
			F	17	67.353	0.743	0.209		
Do	7/12	6_3	M	21	67.476	1.160	0.235	1.376	0.247
			F	23	67.870	1.300	0.237		
Do	7/21	6_3	M	17	67.706	1.343	0.281	0.054	0.815
			F	21	67.619	1.250	0.244		
Do	7/25	6_3	M	29	67.448	1.042	0.189	1.075	0.303
			F	43	67.721	1.302	0.083		
Egegik weir	7/13	6_3	M	48	67.521	0.808	0.129	2.729	0.102
			F	57	67.246	0.653	0.107		
Ugashik weir	7/19	5_2	M	26	67.269	0.444	0.130	1.948	0.166
			F	41	67.512	0.505	0.110		
Kvichak River	7/9	5_2	M	21	67.190	0.860	0.202	2.773	0.105
			F	31	67.548	0.390	0.112		
Do	7/10	5_2	M	23	67.087	0.445	0.139	2.456	0.122
			F	25	67.440	0.508	0.142		
Wood River	7/17	5_2	M	22	67.000	0.381	0.131	0.657	0.425
			F	22	67.182	0.728	0.182		

[1] Significant at 5-percent level.

TABLE B-14. Sexual dimorphism in position of first haemal arch in red salmon collected in 1957.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Tumwater	8/12	4_2	M	17	33.353	0.618	0.190	2.266	0.142
			F	18	33.778	0.770	0.206		
Kodiak Island:									
Karluk weir	9/17	5_3	M	21	34.524	1.060	0.224	1.149	0.289
			F	18	34.222	0.417	0.152		
Red River	6/21	5_2	M	28	34.607	0.618	0.148	0.027	0.866
			F	25	34.640	0.408	0.127		
Do	6/21	5_3	M	36	34.417	0.420	0.108	2.378	0.123
			F	20	34.750	0.931	0.215		
Do	6/21	6_3	M	24	34.458	0.782	0.180	0.000	0.999
			F	22	34.455	0.642	0.170		
Bristol Bay:									
Naknek weir	7/3	6_3	M	17	35.176	1.031	0.246	[1]7.854	0.007
			F	28	34.357	0.829	0.172		
Do	7/5	5_2	M	14	34.357	0.861	0.248	0.324	0.570
			F	15	34.133	0.550	0.191		
Do	7/5	6_3	M	28	34.786	1.137	0.201	0.452	0.505
			F	33	34.455	0.568	0.131		
Do	7/11	6_3	M	17	34.941	0.681	0.200	0.196	0.657
			F	17	34.941	0.681	0.200		
Do	7/12	6_3	M	21	34.571	1.055	0.224	2.377	0.132
			F	23	34.739	1.290	0.236		
Do	7/21	6_3	M	18	34.611	0.841	0.216	2.534	0.119
			F	21	34.619	0.550	0.161		
Do	7/25	6_3	M	30	34.333	0.644	0.155	0.188	0.665
			F	44	34.545	0.811	0.135		
Egegik weir	7/13	6_3	M	49	34.510	0.587	0.109	0.626	0.435
			F	57	34.456	0.644	0.106		
Ugashik weir	7/19	5_2	M	26	34.692	0.620	0.154	0.233	0.628
			F	41	34.805	0.610	0.121		
Kvichak River	7/9	5_2	M	21	34.952	0.550	0.161	2.900	0.093
			F	32	34.781	0.654	0.132		
Do	7/10	5_2	M	23	34.652	0.600	0.161	0.122	0.725
			F	25	34.640	0.741	0.172		
Wood River	7/17	5_2	M	22	34.227	0.281	0.113	0.924	0.346
			F	22	34.591	0.538	0.156		

[1] Significant at 1-percent level.

TABLE B–15. Sexual dimorphism in number of ventral gill rakers in red salmon collected in 1957.

Area	Date	Age group	Sex	*N*	Mean	Variance	Standard error	*F*-value	*P*
Columbia River:									
Tumwater	8/12	4_2	M	17	21.647	0.993	0.241	[1]5.596	0.022
			F	18	20.889	0.811	0.212		
Kodiak Island:									
Karluk weir	9/17	5_3	M	21	22.571	0.755	0.189	1.099	0.303
			F	18	22.889	1.047	0.241		
Red River	6/21	5_2	M	28	22.714	0.951	0.184	0.533	0.471
			F	24	22.917	1.035	0.207		
Do	6/21	5_3	M	37	22.892	0.933	0.158	0.053	0.815
			F	21	22.952	0.850	0.201		
Do	6/21	6_3	M	24	22.500	0.695	0.170	3.876	0.056
			F	22	22.955	0.523	0.154		
Bristol Bay:									
Naknek weir	7/3	6_3	M	17	23.118	0.362	0.146	0.030	0.850
			F	28	23.071	0.959	0.185		
Do	7/5	5_2	M	15	22.600	0.971	0.254	1.638	0.208
			F	14	23.071	0.992	0.266		
Do	7/5	6_3	M	29	22.931	0.567	0.139	0.777	0.386
			F	32	22.750	0.709	0.148		
Do	7/11	6_3	M	18	22.944	0.641	0.188	0.196	0.655
			F	17	22.824	0.656	0.196		
Do	7/12	6_3	M	24	23.417	1.295	0.232	2.377	0.131
			F	24	22.958	0.826	0.185		
Do	7/21	6_3	M	19	23.421	1.033	0.233	2.534	0.120
			F	20	22.950	0.678	0.184		
Do	7/25	6_3	M	30	23.233	1.082	0.190	0.188	0.662
			F	44	23.136	0.772	0.132		
Egegik weir	7/13	6_3	M	49	23.041	0.872	0.133	0.626	0.439
			F	57	22.895	0.917	0.126		
Ugashik weir	7/19	5_2	M	26	22.923	0.712	0.165	0.233	0.627
			F	40	23.025	0.692	0.131		
Kvichak River	7/9	5_2	M	21	23.333	0.635	0.173	2.900	0.094
			F	32	22.969	0.548	0.130		
Do	7/10	5_2	M	23	23.087	0.445	0.139	0.122	0.725
			F	25	23.000	1.000	0.200		
Wood River	7/17	5_2	M	23	22.783	0.540	0.153	0.924	0.346
			F	22	22.545	0.833	0.194		

[1] Significant at 5-percent level.

TABLE B-16. Sexual dimorphism in number of gill rakers in red salmon collected in 1957.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Tumwater	8/12	4_2	M	17	35.412	2.881	0.411	4.171	0.051
			F	18	34.389	1.547	0.293		
Kodiak Island:									
Karluk weir	9/17	5_3	M	21	36.714	1.915	0.302	0.000	0.999
			F	18	36.722	2.211	0.350		
Red River	6/21	5_2	M	28	37.036	1.518	0.232	0.339	0.561
			F	24	37.250	2.021	0.290		
Do	6/21	5_3	M	37	36.973	2.138	0.240	0.660	0.423
			F	21	37.286	1.715	0.285		
Do	6/21	6_3	M	24	36.625	1.026	0.206	1.636	0.202
			F	22	37.045	1.476	0.259		
Bristol Bay:									
Naknek weir	7/3	6_3	M	17	37.529	1.012	0.244	0.296	0.585
			F	28	37.321	1.855	0.257		
Do	7/5	5_2	M	15	36.467	2.278	0.389	0.645	0.433
			F	14	36.929	1.761	0.354		
Do	7/5	6_3	M	29	37.069	1.567	0.232	0.069	0.790
			F	32	37.156	1.748	0.233		
Do	7/11	6_3	M	18	37.222	1.241	0.262	0.857	0.364
			F	17	36.882	1.112	0.255		
Do	7/12	6_3	M	24	37.833	2.665	0.333	1.028	0.318
			F	24	37.417	1.382	0.240		
Do	7/21	6_3	M	19	37.579	2.033	0.327	1.587	0.313
			F	20	37.050	1.415	0.266		
Do	7/25	6_3	M	30	37.367	1.896	0.251	0.265	0.605
			F	44	37.523	1.465	0.182		
Egegik weir	7/13	6_3	M	49	37.224	1.635	0.182	0.067	0.792
			F	57	37.158	1.850	0.180		
Ugashik weir	7/19	5_2	M	26	37.115	1.468	0.237	0.002	0.996
			F	40	37.125	1.241	0.176		
Kvichak River	7/9	5_2	M	21	37.476	0.860	0.202	0.148	0.701
			F	32	37.344	1.909	0.244		
Do	7/10	5_2	M	23	37.391	1.250	0.233	0.673	0.421
			F	25	37.080	2.158	0.293		
Wood River	7/17	5_2	M	23	36.696	1.404	0.247	0.451	0.504
			F	22	36.455	1.500	0.261		

TABLE B–17. Sexual dimorphism in number of branchiostegal rays in red salmon collected in 1957.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Tumwater	8/12	4_2	M	17	13.941	0.681	0.201	[1]4.784	0.033
			F	18	13.278	0.917	0.225		
Kodiak Island:									
Karluk weir	9/17	5_3	M	21	14.190	0.360	0.130	3.332	0.074
			F	18	13.833	0.382	0.145		
Red River	6/21	5_2	M	28	14.179	1.518	0.232	2.520	0.117
			F	25	14.440	0.425	0.130		
Do	6/21	5_3	M	37	14.378	0.463	0.111	0.280	0.595
			F	21	14.286	0.315	0.122		
Do	6/21	6_3	M	24	14.083	0.513	0.146	[1]5.596	0.022
			F	22	14.545	0.357	0.127		
Bristol Bay:									
Naknek weir	7/3	6_3	M	17	13.647	0.993	0.241	0.332	0.564
			F	27	13.778	0.257	0.097		
Do	7/5	5_2	M	15	13.667	0.378	0.158	0.073	0.785
			F	15	13.733	0.492	0.181		
Do	7/5	6_3	M	28	13.786	0.470	0.129	3.239	0.073
			F	33	13.485	0.381	0.107		
Do	7/11	6_3	M	18	13.722	0.477	0.157	0.773	0.387
			F	17	13.529	0.387	0.151		
Do	7/12	6_3	M	24	13.833	0.578	0.155	0.029	0.855
			F	24	13.792	0.782	0.180		
Do	7/21	6_3	M	19	13.684	0.561	0.171	0.016	0.899
			F	21	13.714	0.415	0.140		
Do	7/25	6_3	M	30	13.467	0.465	0.124	0.633	0.433
			F	43	13.605	0.578	0.116		
Egegik weir	7/13	6_3	M	48	13.979	0.617	0.113	0.188	0.661
			F	57	13.912	0.617	0.104		
Ugashik weir	7/19	5_2	M	26	13.846	0.376	0.120	0.071	0.785
			F	41	13.805	0.360	0.093		
Kvichak River	7/9	5_2	M	21	13.857	0.530	0.158	0.048	0.825
			F	31	13.903	0.556	0.134		
Do	7/10	5_2	M	23	13.957	0.227	0.093	0.688	0.416
			F	24	13.792	0.695	0.170		
Wood River	7/17	5_2	M	21	13.667	0.635	0.173	1.402	0.244
			F	22	13.909	0.276	0.112		

[1] Significant at 5-percent level.

TABLE B–18. Sexual dimorphism in number of pectoral-fin rays in red salmon collected in 1957.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Tumwater	8/12	4_2	M	17	15.765	0.193	0.106	1.558	0.220
			F	18	15.944	0.170	0.097		
Kodiak Island:									
Karluk weir	9/17	5_3	M	21	16.429	0.355	0.130	0.498	0.484
			F	18	16.556	0.258	0.119		
Red River	6/21	5_2	M	28	16.536	0.555	0.140	0.965	0.334
			F	24	16.708	0.217	0.095		
Do	6/21	5_3	M	37	16.514	0.366	0.099	0.457	0.500
			F	21	16.619	0.250	0.109		
Do	6/21	6_3	M	24	16.542	0.347	0.120	1.411	0.241
			F	22	16.727	0.209	0.097		
Bristol Bay:									
Naknek weir	7/3	6_3	M	17	16.294	0.218	0.113	0.202	0.650
			F	28	16.214	0.396	0.118		
Do	7/5	5_2	M	15	16.467	0.264	0.132	1.256	0.270
			F	15	16.267	0.207	0.117		
Do	7/5	6_3	M	29	16.379	0.385	0.115	0.008	0.988
			F	33	16.364	0.362	0.104		
Do	7/11	6_3	M	18	16.056	0.405	0.150	0.000	0.999
			F	17	16.059	0.556	0.180		
Do	7/12	6_3	M	24	16.167	0.317	0.115	2.720	0.107
			F	24	16.458	0.434	0.134		
Do	7/21	6_3	M	19	16.211	0.288	0.123	0.020	0.875
			F	21	16.238	0.390	0.136		
Do	7/25	6_3	M	30	16.267	0.341	0.106	0.024	0.873
			F	45	16.244	0.325	0.084		
Egegik weir	7/13	6_3	M	49	16.408	0.287	0.076	0.050	0.820
			F	57	16.386	0.241	0.064		
Ugashik weir	7/19	5_2	M	26	16.462	0.260	0.100	0.108	0.746
			F	41	16.415	0.350	0.092		
Kvichak River	7/9	5_2	M	21	16.619	0.350	0.129	0.048	0.825
			F	32	16.656	0.361	0.106		
Do	7/10	5_2	M	23	16.652	0.236	0.101	1.426	0.239
			F	25	16.480	0.258	0.101		
Wood River	7/17	5_2	M	23	16.522	0.440	0.138	0.403	0.527
			F	22	16.409	0.252	0.107		

TABLE B–19. Sexual dimorphism in number of dorsal-fin elements in red salmon collected in 1957.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
Columbia River:									
Tumwater	8/12	4_2	M	17	14.353	0.368	0.147	0.343	0.560
			F	17	14.235	0.318	0.136		
Kodiak Island:									
Karluk weir	9/17	5_3	M	21	14.619	0.450	0.146	0.048	0.825
			F	18	14.667	0.470	0.161		
Red River	6/21	5_2	M	28	14.964	0.259	0.096	0.728	0.402
			F	25	14.840	0.308	0.111		
Do	6/21	5_3	M	37	15.000	0.388	0.102	0.089	0.765
			F	21	14.952	0.250	0.109		
Do	6/21	6_3	M	24	14.708	0.391	0.127	[1]6.850	0.012
			F	22	15.136	0.219	0.099		
Bristol Bay:									
Naknek weir	7/3	6_3	M	17	15.000	0.250	0.121	0.037	0.842
			F	28	14.964	0.407	0.120		
Do	7/5	5_2	M	15	14.867	0.407	0.164	0.346	0.557
			F	15	14.733	0.350	0.152		
Do	7/5	6_3	M	29	14.966	0.464	0.126	[1]5.746	0.019
			F	33	14.606	0.246	0.086		
Do	7/11	6_3	M	18	14.611	0.252	0.118	0.016	0.900
			F	17	14.588	0.256	0.122		
Do	7/12	6_3	M	24	14.750	0.369	0.124	0.505	0.482
			F	24	14.875	0.373	0.124		
Do	7/21	6_3	M	19	14.632	0.244	0.113	2.014	0.163
			F	21	14.952	0.750	0.189		
Do	7/25	6_3	M	30	14.800	0.441	0.121	0.228	0.632
			F	45	14.733	0.290	0.080		
Egegik weir	7/13	6_3	M	49	14.816	0.277	0.075	0.516	0.475
			F	57	14.895	0.346	0.077		
Ugashik weir	7/19	5_2	M	26	14.615	0.328	0.112	0.137	0.710
			F	41	14.561	0.352	0.092		
Kvichak River	7/9	5_2	M	21	14.714	0.315	0.122	0.185	0.662
			F	32	14.780	0.306	0.097		
Do	7/10	5_2	M	22	14.682	0.228	0.101	2.299	0.160
			F	25	14.960	0.541	0.147		
Wood River	7/17	5_2	M	23	14.522	0.259	0.106	0.175	0.670
			F	22	14.591	0.347	0.125		

[1] Significant at 5-percent level.

TABLE B–20. Sexual dimorphism in number of anal-fin elements in red salmon collected in 1957.

Area	Date	Age group	Sex	N	Mean	Variance	Standard error	F-value	P
lumbia River:									
Tumwater	8/12	4_2	M	17	16.824	2.281	0.366	0.159	0.690
			F	18	17.000	1.176	0.255		
odiak Island:									
Karluk weir	9/17	5_3	M	21	17.905	0.390	0.136	0.385	0.536
			F	18	17.778	0.417	0.152		
Red River	6/21	5_2	M	28	18.250	0.488	0.132	0.034	0.850
			F	25	18.280	0.208	0.091		
Do	6/21	5_3	M	37	18.324	0.391	0.102	1.153	0.297
			F	20	18.500	0.263	0.114		
Do	6/21	6_3	M	24	18.250	0.456	0.137	0.134	0.710
			F	22	18.182	0.347	0.125		
ristol Bay:									
Naknek weir	7/3	6_3	M	17	18.294	0.843	0.222	1.737	0.192
			F	28	17.964	0.555	0.140		
Do	7/5	5_2	M	15	18.067	0.635	0.205	3.146	0.086
			F	15	17.600	0.400	0.163		
Do	7/5	6_3	M	29	18.103	0.453	0.125	0.436	0.512
			F	33	18.000	0.312	0.097		
Do	7/11	6_3	M	18	17.833	0.617	0.185	0.554	0.465
			F	17	18.000	0.250	0.121		
Do	7/12	6_3	M	24	17.958	0.304	0.112	0.985	0.330
			F	24	18.125	0.373	0.124		
Do	7/21	6_3	M	19	17.947	0.716	0.194	0.308	0.577
			F	21	18.095	0.690	0.181		
Do	7/25	6_3	M	30	18.167	0.351	0.108	2.054	0.161
			F	45	17.911	0.718	0.126		
Egegik weir	7/13	6_3	M	48	17.958	0.380	0.089	0.890	0.351
			F	57	18.070	0.351	0.078		
Ugashik weir	7/19	5_2	M	26	18.154	0.296	0.106	1.804	0.183
			F	40	17.950	0.407	0.100		
Kvichak River	7/9	5_2	M	21	17.952	0.350	0.129	0.311	0.572
			F	32	17.875	0.177	0.074		
Do	7/10	5_2	M	23	18.130	0.300	0.114	0.003	0.983
			F	25	18.120	0.358	0.119		
Wood River	7/17	5_2	M	23	18.174	0.331	0.120	2.245	0.142
			F	22	17.909	0.371	0.129		

TABLE B–21. Effect of fresh-water age on number of scales along the lateral line in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	130.333	3.362	0.374	0.831	
	6/22/56	7_4	47	130.723	2.682	0.239		
Do	6/22/56	5_3	15	130.000	5.428	0.602	0.202	
	6/20/57	6_4	14	129.643	3.630	0.509		
Do	6/22/56	6_3	30	130.633	2.310	0.278	1.178	
	6/20/57	7_4	16	130.125	2.246	0.375		
Do	9/7/56	5_3	16	131.063	3.660	0.478	2.119	
	8/21/57 9/9, 17/57	6_4	57	130.351	2.803	0.222		
Red River	6/17, 18/56	4_2	70	130.471	2.803	0.200	0.455	
	6/21/57	5_3	58	130.672	2.820	0.221		
Bristol Bay:								
Egegik weir	7/17/56	4_2	29	129.655	2.164	0.273	0.259	
	7/13/57	5_3	16	129.375	4.913	0.554		
Do	7/17/56	5_2	15	130.067	2.493	0.408	0.311	
	7/13/57	6_3	106	130.377	4.294	0.201		
Ugashik weir	7/23/56	4_2	123	130.244	2.940	0.155	0.981	
	7/19/57	5_3	30	129.900	2.782	0.304		
Kvichak River	7/13/56	4_2	108	130.815	4.376	0.201	3.300	
	7/9, 10/57	5_3	40	131.500	3.538	0.297		

TABLE B–22. Effect of fresh-water age on number of scales below the lateral line in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	20.958	1.346	0.237	3.560	
	6/22/56	7_4	47	20.447	1.078	0.151		
Do	6/22/56	5_3	15	20.067	1.207	0.284	2.799	
	6/20/57	6_4	14	19.500	0.423	0.174		
Do	6/22/56	6_3	30	20.800	2.096	0.264	3.465	
	6/20/57	7_4	16	20.000	1.600	0.100		
Do	9/7/56	5_3	16	19.750	0.733	0.214	2.119	
	8/21/57 9/9, 17/57	6_4	58	20.103	0.866	0.122		
Red River	6/17, 18/56	4_2	70	20.657	0.866	0.111	0.085	
	6/21/57	5_3	58	20.707	0.982	0.130		
Bristol Bay:								
Egegik weir	7/17/56	4_2	29	19.931	0.710	0.156	0.840	
	7/13/57	5_3	16	19.688	0.760	0.218		
Do	7/17/56	5_2	15	20.333	0.378	0.159	3.475	
	7/13/57	6_3	106	19.868	0.877	0.091		
Ugashik weir	7/23/56	4_2	123	19.715	1.008	0.090	[1]9.527	
	7/19/57	5_3	30	19.067	1.306	0.209		
Kvichak River	7/13/56	4_2	109	21.000	0.931	0.095	[1]17.342	<0
	7/9, 10/57	5_3	40	20.225	1.101	0.166		

[1] Significant at 1-percent level.

TABLE B–23. Effect of fresh-water age on number of vertebrae in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	67.292	1.085	0.212	0.140	0.705
	6/22/56	7_4	47	67.213	0.518	0.105		
Do	6/22/56	5_3	15	66.800	0.742	0.222	0.068	0.792
	6/20/57	6_4	14	66.714	0.838	0.244		
Do	6/22/56	6_3	29	67.345	0.521	0.134	0.416	0.522
	6/20/57	7_4	15	67.200	0.457	0.174		
Do	9/7/56	5_3	16	67.563	0.660	0.203	0.175	0.673
	8/21/57 9/9, 17/57	6_4	57	67.474	0.539	0.097		
Red River	6/17, 18/56	4_2	69	67.174	0.528	0.087	2.631	0.107
	6/21/57	5_3	56	67.393	0.606	0.104		
Bristol Bay:								
Egegik weir	7/17/56	4_2	29	67.172	0.503	0.132	0.042	0.830
	7/13/57	5_3	16	67.125	0.646	0.201		
Do	7/17/56	5_2	15	67.067	0.492	0.181	1.723	0.191
	7/13/57	6_3	105	67.371	0.735	0.084		
Ugashik weir	7/23/56	4_2	119	67.277	0.405	0.058	0.109	0.750
	7/19/57	5_3	30	67.233	0.531	0.133		
Kvichak River	7/13/56	4_2	110	67.373	0.676	0.078	[1]4.222	0.045
	7/9, 10/57	5_3	40	67.700	0.933	0.153		

[1] Significant at 5-percent level.

TABLE B–24. Effect of fresh-water age on position of first haemal arch in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	34.625	0.418	0.131	0.764	0.390
	6/22/56	7_4	47	34.468	0.558	0.109		
Do	6/22/56	5_3	15	34.467	0.550	0.183	1.841	0.183
	6/20/57	6_4	14	34.929	1.146	0.286		
Do	6/22/56	6_3	30	34.633	1.206	0.201	0.289	0.592
	6/20/57	7_4	15	34.800	0.457	0.174		
Do	9/7/56	5_3	16	34.375	0.513	0.179	0.880	0.355
	8/21/57 9/9, 17/57	6_4	57	34.596	0.744	0.114		
Red River	6/17, 18/56	4_2	69	34.275	0.526	0.087	3.697	0.055
	6/21/57	5_3	56	34.536	0.616	0.105		
Bristol Bay:								
Egegik weir	7/17/56	4_2	28	34.464	0.629	0.150	0.022	0.875
	7/13/57	5_3	16	34.500	0.533	0.183		
Do	7/17/56	5_2	15	34.067	0.921	0.248	3.471	0.064
	7/13/57	6_3	106	34.481	0.613	0.076		
Ugashik weir	7/23/56	4_2	119	34.580	0.482	0.063	2.140	0.147
	7/19/57	5_3	30	34.800	0.786	0.162		
Kvichak River	7/13/56	4_2	111	34.712	0.807	0.085	0.998	0.322
	7/9, 10/57	5_3	40	34.875	0.722	0.134		

TABLE B–25. Effect of fresh-water age on number of ventral gill rakers in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value
Kodiak Island:							
Karluk weir	6/16, 29/55	6_3	24	22.667	0.753	0.177	0.175
	6/22/56	7_4	47	22.766	0.965	0.143	
Do	6/22/56	5_3	15	22.533	0.550	0.191	0.256
	6/20/57	6_4	14	22.357	1.169	0.289	
Do	6/22/56	6_3	30	22.400	1.420	0.218	0.589
	6/20/57	7_4	16	22.125	1.180	0.272	
Do	9/7/56	5_3	16	22.313	1.293	0.284	3.164
	8/21/57 9/9, 17/57	6_4	58	22.828	0.987	0.130	
Red River	6/17, 18/56	4_2	68	22.824	0.834	0.111	0.297
	6/21/57	5_3	58	22.914	0.887	0.123	
Bristol Bay:							
Egegik weir	7/17/56	4_2	29	23.172	1.217	0.205	0.274
	7/13/57	5_3	16	23.000	0.933	0.242	
Do	7/17/56	5_2	15	22.933	0.778	0.228	0.013
	7/13/57	6_3	106	22.962	0.893	0.092	
Ugashik weir	7/23/56	4_2	119	22.966	0.880	0.085	0.028
	7/19/57	5_3	30	23.000	1.310	0.209	
Kvichak River	7/13/56	4_2	110	23.100	0.769	0.083	0.580
	7/9, 10/57	5_3	40	23.225	0.845	0.145	

TABLE B–26. Effect of fresh-water age on number of gill rakers in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value
Kodiak Island:							
Karluk weir	6/16, 29/55	6_3	24	36.667	1.101	0.214	0.000
	6/22/56	7_4	47	36.660	2.055	0.209	
Do	6/22/56	5_3	15	36.600	2.114	0.375	0.196
	6/20/57	6_4	14	36.357	2.246	0.401	
Do	6/22/56	6_3	30	36.200	2.717	0.301	0.127
	6/20/57	7_4	16	36.375	2.113	0.363	
Do	9/7/56	5_3	16	36.438	2.526	0.397	0.448
	8/21/57 9/9, 17/57	6_4	58	36.724	2.238	0.196	
Red River	6/17, 18/56	4_2	68	37.088	1.514	0.149	0.000
	6/21/57	5_3	58	37.086	1.974	0.184	
Bristol Bay:							
Egegik weir	7/17/56	4_2	29	37.483	2.757	0.308	0.359
	7/13/57	5_3	16	37.188	2.026	0.356	
Do	7/17/56	5_2	15	37.267	1.921	0.358	0.047
	7/13/57	6_3	106	37.189	1.735	0.128	
Ugashik weir	7/23/56	4_2	119	37.109	1.776	0.122	0.141
	7/19/57	5_3	30	37.000	3.034	0.318	
Kvichak River	7/13/56	4_2	110	37.391	1.396	0.112	1.074
	7/9, 10/57	5_3	40	37.625	1.778	0.211	

TABLE B–27. Effect of fresh-water age on number of branchiostegal rays in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	13.958	0.302	0.112	0.000	0.999
	6/22/56	7_4	47	13.957	0.606	0.114		
Do	6/22/56	5_3	15	13.733	0.350	0.153	2.843	0.103
	6/20/57	6_4	14	14.071	0.223	0.126		
Do	6/22/56	6_3	30	13.633	0.448	0.122	[1]4.124	0.050
	6/20/57	7_4	16	14.000	0.133	0.091		
Do	9/7/56	5_3	16	13.875	0.513	0.179	0.085	0.767
	8/21/57 9/9, 17/57	6_4	58	13.931	0.450	0.088		
Red River	6/17, 18/56	4_2	70	14.214	0.518	0.086	1.156	0.284
	6/21/57	5_3	58	14.345	0.405	0.083		
Bristol Bay:								
Egegik weir	7/17/56	4_2	28	13.750	0.266	0.098	2.944	0.096
	7/13/57	5_3	16	14.063	0.460	0.169		
Do	7/17/56	5_2	15	14.400	0.828	0.235	[1]4.307	0.044
	7/13/57	6_3	105	13.943	0.612	0.076		
Ugashik weir	7/23/56	4_2	118	13.890	0.355	0.055	0.227	0.631
	7/19/57	5_3	29	13.828	0.575	0.141		
Kvichak River	7/13/56	4_2	111	13.766	0.526	0.069	3.389	0.070
	7/9, 10/57	5_3	40	14.025	0.742	0.136		

[1] Significant at 5-percent level.

TABLE B–28. Effect of fresh-water age on number of pectoral-fin rays in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	16.167	0.231	0.098	2.286	0.141
	6/22/56	7_4	47	16.383	0.371	0.089		
Do	6/22/56	5_3	15	16.533	0.264	0.133	0.262	0.608
	6/20/57	6_4	14	16.643	0.400	0.169		
Do	6/22/56	6_3	30	16.633	0.241	0.089	0.744	0.398
	6/20/57	7_4	16	16.500	0.266	0.129		
Do	9/7/56	5_3	16	16.625	0.246	0.124	0.187	0.662
	8/21/57 9/9, 17/57	6_4	58	16.690	0.287	0.070		
Red River	6/17, 18/56	4_2	70	16.443	0.308	0.066	1.195	0.276
	6/21/57	5_3	58	16.552	0.321	0.074		
Bristol Bay:								
Egegik weir	7/17/56	4_2	29	16.586	0.607	0.145	0.540	0.468
	7/13/57	5_3	16	16.750	0.333	0.144		
Do	7/17/56	5_2	15	16.800	0.171	0.107	[1]8.568	0.004
	7/13/57	6_3	106	16.396	0.260	0.049		
Ugashik weir	7/23/56	4_2	120	16.492	0.268	0.047	2.946	0.090
	7/19/57	5_3	30	16.300	0.424	0.119		
Kvichak River	7/13/56	4_2	110	16.518	0.417	0.061	0.077	0.777
	7/9, 10/57	5_3	40	16.550	0.305	0.087		

[1] Significant at 1-percent level.

TABLE B–29. Effect of fresh-water age on number of dorsal-fin elements in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	14.583	0.514	0.146	0.184	0
	6/22/56	7_4	47	14.511	0.429	0.095		
Do	6/22/56	5_3	15	14.600	0.257	0.131	0.053	0
	6/20/57	6_4	14	14.643	0.246	0.132		
Do	6/22/56	6_3	30	14.600	0.317	0.102	0.923	0
	6/20/57	7_4	16	14.438	0.260	0.127		
Do	9/7/56	5_3	16	14.375	0.246	0.124	2.952	0
	8/21/57 9/9, 17/57	6_4	58	14.638	0.305	0.072		
Red River	6/17, 18/56	4_2	70	14.357	0.523	0.086	[1]28.412	<0
	6/21/57	5_3	58	14.983	0.333	0.076		
Bristol Bay:								
Egegik weir	7/17/56	4_2	29	14.862	0.407	0.118	0.715	0
	7/13/57	5_3	16	14.688	0.493	0.176		
Do	7/17/56	5_2	15	14.400	0.542	0.190	[1]8.121	0
	7/13/57	6_3	106	14.858	0.313	0.054		
Ugashik weir	7/23/56	4_2	118	14.492	0.354	0.055	[1]12.091	<0
	7/19/57	5_3	30	14.900	0.231	0.088		
Kvichak River	7/13/56	4_2	109	14.798	0.347	0.056	0.982	0
	7/9, 10/57	5_3	39	14.692	0.271	0.083		

[1] Significant at 1-percent level.

TABLE B–30. Effect of fresh-water age on number of anal-fin elements in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	18.000	0.521	0.147	2.470	0
	6/22/56	7_4	47	17.745	0.368	0.088		
Do	6/22/56	5_3	15	17.800	0.314	0.145	0.004	0
	6/20/57	6_4	14	17.786	0.338	0.155		
Do	6/22/56	6_3	30	17.833	0.351	0.108	0.330	0
	6/20/57	7_4	16	17.938	0.326	0.143		
Do	9/7/56	5_3	16	18.063	0.326	0.143	0.545	0
	8/21/57 9/9, 17/57	6_4	58	17.931	0.415	0.084		
Red River	6/17, 18/56	4_2	70	18.086	0.398	0.075	[1]7.534	0
	6/21/57	5_3	57	18.386	0.348	0.078		
Bristol Bay:								
Egegik weir	7/17/56	4_2	29	18.034	0.321	0.105	[1]7.463	0
	7/13/57	5_3	16	18.625	0.780	0.221		
Do	7/17/56	5_2	15	17.800	0.600	0.200	1.603	0
	7/13/57	6_3	105	18.019	0.365	0.058		
Ugashik weir	7/23/56	4_2	119	17.908	0.254	0.046	0.059	0
	7/19/57	5_3	30	17.933	0.341	0.106		
Kvichak River	7/13/56	4_2	109	17.862	0.434	0.062	1.718	0
	7/9, 10/57	5_3	38	18.026	0.458	0.110		

[1] Significant at 1-percent level.

TABLE B–31. Effect of ocean age on number of scales along the lateral line in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
Kodiak Island:								
Karluk weir	6/16, 29/55	6_4	38	129.553	3.713	0.313	[1]9.166	0.004
	6/22/56	7_4	47	130.723	2.682	0.239		
Do	6/22/56	6_4	55	129.891	3.136	0.239	0.231	0.627
	6/20/57	7_4	16	130.012	2.246	0.375		
Red River	6/17, 18/56	4_2	70	130.471	2.803	0.200	3.858	0.055
	6/21/57	5_2	53	131.038	2.113	0.199		
Do	6/18/56	5_3	31	131.290	3.280	0.325	0.238	0.623
	6/21/57	6_3	46	131.109	2.099	0.214		
Bristol Bay:								
Naknek weir	7/6, 8/56	5_3	30	131.333	5.885	0.443	1.075	0.298
	7/3–29/57	6_3	324	130.901	4.751	0.383		
Egegik weir	7/17/56	4_2	29	129.655	2.164	0.273	1.378	0.247
	7/13/57	5_2	17	130.176	2.031	0.346		
Do	7/17/56	5_3	110	130.009	2.467	0.150	2.176	0.144
	7/13/57	6_3	106	130.377	4.294	0.202		
Ugashik weir	7/23/56	4_2	123	130.244	2.940	0.154	1.303	0.257
	7/19/57	5_2	67	130.522	1.919	0.169		
Kvichak River	7/13/56	4_2	108	130.815	4.376	0.202	0.319	0.570
	7/9/57	5_2	53	131.000	2.692	0.225		
Do	7/13/56	4_2	108	130.815	4.376	0.202	0.004	0.985
	7/10/57	5_2	48	130.792	2.849	0.244		
Wood River	7/11/56	4_2	118	129.864	3.519	0.173	0.892	0.350
	7/17/57	5_2	45	129.556	3.388	0.274		

[1] Significant at 1-percent level.

TABLE B–32. Effect of ocean age on number of scales below the lateral line in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
Kodiak Island:								
Karluk weir	6/16, 29/55	6_4	38	20.053	1.780	0.216	2.346	0.131
	6/22/56	7_4	47	20.447	1.078	0.151		
Do	6/22/56	6_4	55	19.709	1.284	0.153	0.755	0.393
	6/20/57	7_4	16	20.000	1.600	0.312		
Red River	6/17, 18/56	4_2	70	20.657	0.866	0.111	[1]4.473	0.042
	6/21/57	5_2	53	21.019	0.903	0.130		
Do	6/18/56	5_3	31	20.677	0.826	0.163	0.028	0.860
	6/21/57	6_3	46	20.717	1.229	0.163		
Bristol Bay:								
Naknek weir	7/6, 8/56	5_3	30	20.133	1.774	0.243	[1]4.384	0.044
	7/3–29/57	6_3	324	19.741	0.895	0.423		
Egegik weir	7/17/56	4_2	29	19.931	0.710	0.156	[1]6.525	0.014
	7/13/57	5_2	17	20.706	1.468	0.294		
Do	7/17/56	5_3	111	20.000	1.054	0.098	0.977	0.327
	7/13/57	6_3	106	19.868	0.877	0.090		
Ugashik weir	7/23/56	4_2	123	19.715	1.008	0.090	0.273	0.600
	7/19/57	5_2	67	19.642	0.597	0.094		
Kvichak River	7/13/56	4_2	109	21.000	0.981	0.094	1.407	0.238
	7/9/57	5_2	53	20.792	1.321	0.158		
Do	7/13/56	4_2	109	21.000	0.981	0.095	[1]4.023	0.048
	7/10/57	5_2	48	20.667	0.780	0.127		
Wood River	7/11/56	4_2	118	20.322	0.886	0.087	0.218	0.640
	7/17/57	5_2	45	20.400	0.972	0.147		

[1] Significant at 5-percent level.

TABLE B–33. Effect of ocean age on number of vertebrae in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	
Kodiak Island:								
Karluk weir	6/16, 29/55	6_4	38	67.053	0.753	0.141	0.864	0.
	6/22/56	7_4	47	67.213	0.518	0.105		
Do	6/22/56	6_4	55	67.891	0.654	0.109	1.834	0.
	6/20/57	7_4	15	67.200	0.457	0.174		
Red River	6/17, 18/56	4_2	69	67.174	0.528	0.087	[1]7.950	0.
	6/21/57	5_2	53	67.547	0.521	0.099		
Do	6/18/56	5_3	31	67.677	0.493	0.126	1.206	0.
	6/21/57	6_3	46	67.500	0.477	0.102		
Bristol Bay:								
Naknek weir	7/6, 8/56	5_3	30	67.667	1.195	0.199	0.389	0.
	7/3–29/57	6_3	309	67.547	0.980	0.056		
Egegik weir	7/17/56	4_2	29	67.172	0.503	0.131	1.334	0.
	7/13/57	5_2	17	67.412	0.381	0.150		
Do	7/17/56	5_3	111	67.234	0.526	0.068	1.616	0.
	7/13/57	6_3	105	67.371	0.735	0.084		
Ugashik weir	7/23/56	4_2	119	67.277	0.405	0.058	1.947	0.
	7/19/57	5_2	67	67.418	0.489	0.085		
Kvichak River	7/13/56	4_2	110	67.373	0.676	0.078	0.052	0.
	7/9/57	5_2	52	67.404	0.598	0.107		
Do	7/13/56	4_2	110	67.373	0.676	0.078	0.524	0.
	7/10/57	5_2	48	67.271	0.627	0.114		
Wood River	7/11/56	4_2	118	67.254	0.601	0.077	1.454	0.
	7/17/57	5_2	44	67.091	0.549	0.111		

[1] Significant at 1-percent level.

TABLE B–34. Effect of ocean age on position of first haemal arch in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	
Kodiak Island:								
Karluk weir	6/16, 29/55	6_4	38	34.737	1.009	0.163	1.998	0.
	6/22/56	7_4	47	34.468	0.558	0.109		
Do	6/22/56	6_4	55	34.564	0.509	0.096	1.319	0.
	6/20/57	7_4	15	34.800	0.457	0.174		
Red River	6/17, 18/56	4_2	69	34.275	0.526	0.087	[1]6.972	0.
	6/21/57	5_2	53	34.623	0.508	0.098		
Do	6/18/56	5_3	31	34.806	0.826	0.163	3.024	0.
	6/21/57	6_3	46	34.456	0.698	0.123		
Bristol Bay:								
Naknek weir	7/6, 8/56	5_3	30	34.700	0.837	0.167	0.120	0.
	7/3–29/57	6_3	316	34.639	0.836	0.414		
Egegik weir	7/17/56	4_2	28	34.464	0.629	0.150	1.002	0.
	7/13/57	5_2	17	34.706	0.593	0.187		
Do	7/17/56	5_3	111	34.568	0.465	0.064	0.752	0.
	7/13/57	6_3	106	34.481	0.613	0.076		
Ugashik weir	7/23/56	4_2	119	34.580	0.482	0.063	2.671	0.
	7/19/57	5_2	67	34.761	0.608	0.095		
Kvichak River	7/13/56	4_2	111	34.712	0.807	0.085	0.933	0.
	7/9/57	5_2	53	34.849	0.553	0.102		
Do	7/13/56	4_2	111	34.712	0.807	0.085	0.191	0.
	7/10/57	5_2	48	34.646	0.659	0.117		
Wood River	7/11/56	4_2	118	34.339	0.619	0.072	0.277	0.
	7/17/57	5_2	48	34.409	0.433	0.095		

[1] Significant at 1-percent level.

TABLE B–35. Effect of ocean age on number of ventral gill rakers in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
Kodiak Island:								
Karluk weir	6/16, 29/55	6_4	38	22.316	0.708	0.136	[1]5.003	0.028
	6/22/56	7_4	47	22.766	0.965	0.143		
Do	6/22/56	6_4	55	22.364	0.569	0.101	1.005	0.325
	6/20/57	7_4	16	22.125	1.180	0.271		
Red River	6/17, 18/56	4_2	68	22.824	0.834	0.110	0.008	0.933
	6/21/57	5_2	52	22.808	0.981	0.137		
Do	6/18/56	5_3	31	22.871	1.050	0.184	0.539	0.467
	6/21/57	6_3	46	22.717	0.651	0.119		
Bristol Bay:								
Naknek weir	7/6, 8/56	5_3	29	23.172	0.647	0.149	0.370	0.542
	7/3–29/57	6_3	322	23.065	0.835	0.409		
Egegik weir	7/17/56	4_2	29	23.172	1.217	0.205	1.923	0.174
	7/13/57	5_2	16	22.750	0.466	0.170		
Do	7/17/56	5_3	110	23.046	0.887	0.089	0.419	0.516
	7/13/57	6_3	106	22.962	0.893	0.092		
Ugashik weir	7/23/56	4_2	119	22.966	0.880	0.085	0.018	0.879
	7/19/57	5_2	66	22.985	0.692	0.102		
Kvichak River	7/13/56	4_2	110	23.100	0.769	0.083	0.009	0.928
	7/9/57	5_2	53	23.113	0.602	0.106		
Do	7/13/56	4_2	110	23.100	0.769	0.083	0.151	0.695
	7/10/57	5_2	48	23.042	0.721	0.126		
Wood River	7/11/56	4_2	118	22.636	0.746	0.079	0.043	0.832
	7/17/57	5_2	45	22.667	0.681	0.123		

[1] Significant at 5-percent level.

TABLE B–36. Effect of ocean age on number of gill rakers in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
Kodiak Island:								
Karluk weir	6/16, 29/55	6_4	38	35.974	1.539	0.101	[1]5.415	0.022
	6/22/56	7_4	47	36.660	2.055	0.209		
Do	6/22/56	6_4	53	36.189	1.386	0.161	0.275	0.598
	6/20/57	7_4	16	36.375	2.113	0.363		
Red River	6/17, 18/56	4_2	68	37.088	1.514	0.149	0.039	0.837
	6/21/57	5_2	52	37.135	1.726	0.182		
Do	6/18/56	5_3	31	36.806	1.760	0.238	0.005	0.964
	6/21/57	6_3	46	36.826	1.257	0.165		
Bristol Bay:								
Naknek weir	7/6, 8/56	5_3	29	37.207	1.384	0.218	0.283	0.593
	7/3–29/57	6_3	321	37.338	1.598	0.606		
Egegik weir	7/17/56	4_2	29	37.483	2.757	0.308	0.585	0.453
	7/13/57	5_2	16	37.125	1.313	0.286		
Do	7/17/56	5_3	110	37.300	1.955	0.133	0.362	0.594
	7/13/57	6_3	106	37.189	1.735	0.128		
Ugashik weir	7/23/56	4_2	119	37.109	1.776	0.122	0.003	0.969
	7/19/57	5_2	66	37.121	1.308	0.141		
Kvichak River	7/13/56	4_2	110	37.391	1.396	0.112	0.001	0.999
	7/9/57	5_2	53	37.396	1.474	0.167		
Do	7/13/56	4_2	110	37.391	1.396	0.112	0.586	0.499
	7/10/57	5_2	48	37.229	1.712	0.189		
Wood River	7/11/56	4_2	118	36.500	1.841	0.125	0.114	0.733
	7/17/57	5_2	45	36.578	1.431	0.178		

[1] Significant at 5-percent level.

TABLE B–37. Effect of ocean age on number of branchiostegal rays in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value
Kodiak Island:							
Karluk weir	6/16, 29/55	6_4	38	13.790	0.495	0.114	1.064
	6/22/56	7_4	47	13.957	0.606	0.114	
Do	6/22/56	6_4	55	13.436	0.509	0.096	[1]9.202
	6/20/57	7_4	16	14.000	0.133	0.091	
Red River	6/17, 18/56	4_2	70	14.214	0.518	0.086	0.509
	6/21/57	5_2	53	14.302	0.368	0.083	
Do	6/18/56	5_3	31	14.387	0.446	0.120	0.271
	6/21/57	6_3	46	14.304	0.483	0.102	
Bristol Bay:							
Naknek weir	7/6, 8/56	5_3	30	13.600	0.524	0.132	0.194
	7/3–29/57	6_3	321	13.660	0.514	0.300	
Egegik weir	7/17/56	4_2	28	13.750	0.266	0.098	[1]8.703
	7/13/57	5_2	17	14.235	0.318	0.137	
Do	7/17/56	5_3	111	13.748	0.390	0.059	[2]4.124
	7/13/57	6_3	105	13.943	0.612	0.076	
Ugashik weir	7/23/56	4_2	118	13.890	0.355	0.055	0.568
	7/19/57	5_2	67	13.821	0.361	0.073	
Kvichak River	7/13/56	4_2	111	13.766	0.526	0.069	0.945
	7/9/57	5_2	52	13.885	0.535	0.101	
Do	7/13/56	4_2	111	13.766	0.526	0.069	0.739
	7/10/57	5_2	47	13.872	0.461	0.099	
Wood River	7/11/56	4_2	117	13.598	0.535	0.067	2.264
	7/17/57	5_2	43	13.791	0.455	0.102	

[1] Significant at 1-percent level.
[2] Significant at 5-percent level.

TABLE B–38. Effect of ocean age on number of pectoral-fin rays in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value
Kodiak Island:							
Karluk weir	6/16, 29/55	6_4	38	16.316	0.330	0.093	0.269
	6/22/56	7_4	47	16.383	0.371	0.089	
Do	6/22/56	6_4	55	16.491	0.328	0.077	0.008
	6/20/57	7_4	16	16.500	0.266	0.129	
Red River	6/17, 18/56	4_2	70	16.443	0.308	0.066	2.563
	6/21/57	5_2	52	16.615	0.398	0.087	
Do	6/18/56	5_3	31	16.581	0.316	0.101	0.154
	6/21/57	6_3	46	16.630	0.282	0.078	
Bristol Bay:							
Naknek weir	7/6, 8/56	5_3	30	16.167	0.212	0.084	0.800
	7/3–29/57	6_3	325	16.267	0.361	0.303	
Egegik weir	7/17/56	4_2	29	16.586	0.607	0.145	0.300
	7/13/57	5_2	17	16.706	0.343	0.142	
Do	7/17/56	5_3	111	16.486	0.306	0.052	0.589
	7/13/57	6_3	106	16.396	0.260	0.049	
Ugashik weir	7/23/56	4_2	120	16.492	0.268	0.047	0.525
	7/19/57	5_2	67	16.642	0.309	0.068	
Kvichak River	7/13/56	4_2	110	16.518	0.417	0.061	1.376
	7/9/57	5_2	53	16.642	0.349	0.081	
Do	7/13/56	4_2	110	16.518	0.417	0.061	0.179
	7/10/57	5_2	48	16.562	0.251	0.072	
Wood River	7/11/56	4_2	118	16.339	0.345	0.054	1.537
	7/17/57	5_2	45	16.467	0.345	0.087	

TABLE B–39. Effect of ocean age on number of dorsal-fin elements in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
Kodiak Island:								
Karluk weir	6/16, 29/55	6_4	38	14.500	0.310	0.089	0.006	0.965
	6/22/56	7_4	47	14.511	0.429	0.095		
Do	6/22/56	6_4	55	14.709	0.395	0.084	2.495	0.118
	6/20/57	7_4	16	14.438	0.260	0.127		
Red River	6/17, 18/56	4_2	70	14.357	0.523	0.086	[1]21.701	<0.001
	6/21/57	5_2	53	14.906	0.279	0.072		
Do	6/18/56	5_3	31	14.677	0.360	0.108	2.918	0.092
	6/21/57	6_3	46	14.913	0.347	0.087		
Bristol Bay:								
Naknek weir	7/6, 8/56	5_3	28	14.643	0.386	0.117	1.617	0.206
	7/3–29/57	6_3	325	14.794	0.358	0.303		
Egegik weir	7/17/56	4_2	29	14.862	0.407	0.118	0.039	0.836
	7/13/57	5_2	17	14.824	0.406	0.155		
Do	7/17/56	5_3	111	14.685	0.308	0.042	[2]5.268	0.024
	7/13/57	6_3	106	14.858	0.313	0.054		
Ugashik weir	7/23/56	4_2	118	14.492	0.354	0.055	1.005	0.319
	7/19/57	5_2	67	14.582	0.337	0.061		
Kvichak River	7/13/56	4_2	109	14.798	0.347	0.056	0.201	0.651
	7/9/57	5_2	53	14.755	0.304	0.076		
Do	7/13/56	4_2	109	14.798	0.347	0.056	0.090	0.760
	7/10/57	5_2	47	14.830	0.405	0.093		
Wood River	7/11/56	4_2	116	14.612	0.378	0.057	0.291	0.587
	7/17/57	5_2	45	14.556	0.298	0.081		

[1] Significant at 1-percent level.
[2] Significant at 5-percent level.

TABLE B–40. Effect of ocean age on number of anal-fin elements in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
Kodiak Island:								
Karluk weir	6/16, 29/55	6_4	38	17.947	0.321	0.092	2.485	0.119
	6/22/56	7_4	47	17.745	0.368	0.088		
Do	6/22/56	6_4	55	17.909	0.380	0.083	0.027	0.856
	6/20/57	7_4	16	17.938	0.326	0.143		
Red River	6/17, 18/56	4_2	70	18.086	0.398	0.075	2.538	0.114
	6/21/57	5_2	53	18.264	0.351	0.081		
Do	6/18/56	5_3	28	18.214	0.470	0.130	0.000	0.999
	6/21/57	6_3	46	18.217	0.396	0.093		
Bristol Bay:								
Naknek weir	7/6, 8/56	5_3	30	17.867	0.533	0.133	1.536	0.215
	7/3–29/57	6_3	316	18.490	0.516	0.304		
Egegik weir	7/17/56	4_2	29	18.034	0.321	0.105	2.448	0.125
	7/13/57	5_2	17	17.765	0.318	0.137		
Do	7/17/56	5_3	110	17.909	0.376	0.058	1.751	0.187
	7/13/57	6_3	105	18.019	0.365	0.058		
Ugashik weir	7/23/56	4_2	119	17.908	0.254	0.046	2.171	0.194
	7/19/57	5_2	66	18.030	0.368	0.074		
Kvichak River	7/13/56	4_2	109	17.862	0.434	0.062	0.179	0.667
	7/9/57	5_2	53	17.906	0.240	0.067		
Do	7/13/56	4_2	109	17.862	0.434	0.062	[1]5.729	0.021
	7/10/57	5_2	48	18.125	0.324	0.082		
Wood River	7/11/56	4_2	117	18.008	0.474	0.063	0.095	0.753
	7/17/57	5_2	45	18.044	0.361	0.089		

[1] Significant at 5-percent level.

TABLE B–41. Effect of brood year on number of scales along the lateral line in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	130.333	3.362	0.374	0.432	0
	6/22/56	6_3	30	130.633	2.310	0.277		
Do	6/16, 29/55	6_4	38	129.553	3.713	0.312	0.763	0
	6/22/56	6_4	55	129.891	3.136	0.239		
Do	6/22/56	5_3	15	130.000	5.428	0.602	0.569	0
	6/20/57	5_3	33	129.576	2.315	0.265		
Do	8/24/55	6_4	18	130.889	2.576	0.378	1.119	0
	9/7/56	6_4	68	130.794	3.986	0.242		
	8/21/57, 9/9, 17/57	6_4	57	130.351	2.803	0.222		
Do	9/7/56	5_3	16	131.063	3.660	0.478	3.870	0
	8/21/57, 9/9, 17/57	5_3	58	130.103	3.550	0.247		
Red River	6/18/55	6_3	17	131.059	2.681	0.397	0.008	0
	6/17, 18/56	6_3	39	131.128	5.641	0.380		
	6/21/57	6_3	46	131.109	2.099	0.214		
Do	6/18/56	5_3	31	131.290	3.280	0.325	2.589	0
	6/21/57	5_3	58	130.672	2.820	0.220		
Bristol Bay:								
Egegik weir	7/17/56	5_2	17	130.176	2.031	0.346	0.043	0
	7/13/57	5_2	15	130.067	2.492	0.308		
Do	7/17/56	5_3	16	129.375	4.913	0.548	2.032	0
	7/13/57	5_3	110	130.009	2.467	0.150		
Do	7/17/56	6_3	16	130.250	4.600	0.536	0.052	0
	7/13/57	6_3	106	130.377	4.294	0.201		
Ugashik weir	7/23/56	4_2	30	130.933	4.065	0.368	3.632	0
	7/19/57	4_2	123	130.244	2.940	0.155		
Do	7/23/56	5_3	35	129.743	3.843	0.346	0.119	0
	7/19/57	5_3	30	129.900	2.782	0.304		
Kvichak River	7/13/56	5_3	53	131.528	3.946	0.273	0.078	0
	7/10/57	5_3	29	131.655	3.735	0.359		

TABLE B–42. Effect of brood year on number of scales below the lateral line in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
diak Island:								
Karluk weir	6/16, 29/55	6_3	24	20.958	1.346	0.237	0.189	0.661
	6/22/56	6_3	30	20.800	2.096	0.264		
Do	6/16, 29/55	6_4	38	20.053	3.136	0.287	1.785	0.184
	6/22/56	6_4	55	19.709	1.780	0.180		
Do	6/22/56	5_3	15	20.067	1.207	0.284	1.022	0.318
	6/20/57	5_3	33	19.727	1.140	0.186		
Do	8/24/55	6_4	18	20.889	1.870	0.322	[1]10.483	<0.001
	9/7/56	6_4	69	19.696	0.920	0.115		
	8/21/57, 9/9, 17/57	6_4	58	20.103	0.866	0.122		
Do	9/7/56	5_3	16	19.750	0.733	0.214	1.172	0.280
	8/21/57, 9/9, 17/57	5_3	67	20.209	2.683	0.200		
Red River	6/18/55	6_3	17	20.765	1.318	0.278	0.193	0.894
	6/17, 18/56	6_3	39	20.872	1.430	0.191		
	6/21/57	6_3	46	20.717	1.229	0.163		
Do	6/18/56	5_3	31	20.677	0.826	0.163	0.019	0.880
	6/21/57	5_3	58	20.707	0.982	0.130		
ristol Bay:								
Egegik weir	7/17/56	5_2	17	20.706	1.468	0.294	1.150	0.292
	7/13/57	5_2	15	20.333	0.378	0.159		
Do	7/17/56	5_3	16	19.688	0.760	0.218	1.340	0.251
	7/13/57	5_3	111	20.000	1.054	0.097		
Do	7/17/56	6_3	16	20.125	1.046	0.256	1.022	0.314
	7/13/57	6_3	106	19.868	0.877	0.091		
Ugashik weir	7/23/56	4_2	123	19.715	1.008	0.090	[2]6.671	0.011
	7/19/57	4_2	30	20.233	0.806	0.164		
Do	7/23/56	5_3	35	19.257	1.137	0.180	0.482	0.490
	7/19/57	5_3	30	19.067	1.306	0.208		
Kvichak River	7/13/56	5_3	29	20.379	1.171	0.201	0.414	0.523
	7/10/57	5_3	53	20.547	1.329	0.158		

[1] Significant at 1-percent level.
[2] Significant at 5-percent level.

TABLE B–43. Effect of brood year on number of vertebrae in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	67.292	1.085	0.213	0.048	
	6/22/50	6_3	29	67.345	0.521	0.134		
Do	6/16, 29/55	6_4	38	67.053	0.753	0.139	0.846	
	6/22/56	6_4	55	66.891	0.654	0.109		
Do	6/22/56	5_3	15	66.800	0.742	0.222	0.857	
	6/20/57	5_3	33	67.030	0.593	0.134		
Do	8/24/55	6_4	18	67.444	1.435	0.282	0.214	
	9/7/56	6_4	67	67.373	0.752	0.106		
	8/21/57, 9/9, 17/57	6_4	57	67.474	0.539	0.097		
Do	9/7/56	5_3	16	67.563	0.660	0.203	1.288	
	8/21/57, 9/9, 17/57	5_3	66	67.303	0.675	0.101		
Red River	6/18/55	6_3	17	67.471	0.512	0.173	0.015	
	6/17, 18/56	6_3	38	67.474	0.850	0.149		
	6/21/57	6_3	46	67.500	0.477	0.101		
Do	6/18/56	5_3	31	67.677	0.493	0.126	2.854	
	6/21/57	5_3	56	67.393	0.606	0.104		
Bristol Bay:								
Egegik weir	7/17/56	5_2	17	67.412	0.381	0.150	2.181	
	7/13/57	5_2	15	67.067	0.492	0.181		
Do	7/17/56	5_3	16	67.125	0.650	0.201	0.031	
	7/13/57	5_3	111	67.234	0.526	0.068		
Do	7/17/56	6_3	16	67.188	0.826	0.227	0.628	
	7/13/57	6_3	105	67.371	0.735	0.084		
Ugashik weir	7/23/56	4_2	119	67.277	0.405	0.058	0.791	
	7/19/57	4_2	30	67.400	0.662	0.148		
Do	7/23/56	5_3	34	67.265	0.624	0.135	0.027	
	7/19/57	5_3	30	67.233	0.531	0.133		
Kvichak River	7/13/56	5_3	29	67.793	1.100	0.195	0.643	
	7/10/57	5_3	51	67.608	0.923	0.134		

TABLE B–44. Effect of brood year on position of first haemal arch in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	34.625	0.418	0.132	0.001	0.999
	6/22/56	6_3	30	34.633	1.206	0.200		
Do	6/16, 29/55	6_4	38	34.734	1.009	0.163	0.945	0.333
	6/22/56	6_4	55	34.564	0.509	0.096		
Do	6/22/56	5_3	15	34.467	0.550	0.191	0.046	0.827
	6/20/57	5_3	33	34.515	0.506	0.124		
Do	8/24/55	6_4	18	34.778	0.770	0.207	0.679	0.490
	9/7/56	6_4	67	34.508	0.829	0.111		
	8/21/57, 9/9, 17/57	6_4	57	34.596	0.744	0.114		
Do	9/7/56	5_3	16	34.375	0.513	0.179	0.067	0.792
	8/21/57, 9/9, 17/57	5_3	66	34.439	0.866	0.114		
Red River	6/18/55	6_3	17	34.647	0.493	0.170	0.641	0.540
	6/17, 18/56	6_3	38	34.632	0.617	0.127		
	6/21/57	6_3	46	34.456	0.698	0.123		
Do	6/18/56	5_3	31	34.806	0.826	0.163	2.115	0.151
	6/21/57	5_3	56	34.536	0.616	0.105		
Bristol Bay:								
Egegik weir	7/17/56	5_2	17	34.706	0.593	0.187	[1]4.348	0.046
	7/13/57	5_2	15	34.067	0.921	0.248		
Do	7/17/56	5_3	16	34.500	0.533	0.182	0.134	0.711
	7/13/57	5_3	111	34.568	0.465	0.064		
Do	7/17/56	6_3	16	34.375	1.313	0.286	0.223	0.634
	7/13/57	6_3	106	34.481	0.613	0.075		
Ugashik weir	7/23/56	4_2	30	34.633	0.586	0.140	0.136	0.710
	7/19/57	4_2	119	34.580	0.482	0.063		
Do	7/23/56	5_3	34	34.382	0.667	0.140	3.845	0.055
	7/19/57	5_3	30	34.800	0.786	0.162		
Kvichak River	7/13/56	5_3	51	34.863	0.680	0.115	0.028	0.856
	7/10/57	5_3	29	34.897	0.882	0.174		

[1] Significant at 5-percent level.

TABLE B–45. Effect of brood year on number of ventral gill rakers in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	22.667	0.753	0.177	0.842	
	6/22/56	6_3	30	22.400	1.420	0.214		
Do	6/16, 29/55	6_4	38	22.316	0.708	0.136	0.082	
	6/22/56	6_4	55	22.364	0.569	0.101		
Do	6/22/56	5_3	15	22.533	0.550	0.191	0.025	
	6/20/57	5_3	33	22.485	1.131	0.185		
Do	8/24/55	6_4	18	22.444	0.964	0.231	1.371	
	9/7/56	6_4	69	22.609	0.918	0.115		
	8/21/57, 9/9, 17/57	6_4	58	22.828	0.987	0.130		
Do	9/7/56	5_3	16	22.313	1.293	0.284	2.982	
	8/21/57, 9/9, 17/57	5_3	68	22.750	0.728	0.103		
Red River	6/18/55	6_3	17	23.000	1.125	0.257	2.005	
	6/17, 18/56	6_3	40	22.500	0.769	0.138		
	6/21/57	6_3	46	22.717	0.651	0.119		
Do	6/18/56	5_3	31	22.871	1.050	0.184	0.039	
	6/21/57	5_3	58	22.914	0.887	0.123		
Bristol Bay:								
Egegik weir	7/17/56	5_2	16	22.750	0.466	0.170	0.421	
	7/13/57	5_2	15	22.933	0.778	0.228		
Do	7/17/56	5_3	16	23.000	0.933	0.241	0.032	
	7/13/57	5_3	110	23.046	0.887	0.894		
Do	7/17/56	6_3	16	22.938	0.993	0.249	0.009	
	7/13/57	6_3	106	22.962	0.893	0.092		
Ugashik weir	7/23/56	4_2	119	22.966	0.880	0.085	0.000	
	7/19/57	4_2	30	22.967	1.275	0.206		
Do	7/23/56	5_3	34	22.765	0.670	0.140	0.910	
	7/19/57	5_3	30	23.000	1.310	0.209		
Kvichak River	7/13/56	5_3	29	23.379	0.814	0.167	2.317	
	7/10/57	5_3	52	23.058	0.839	0.127		

TABLE B–46. Effect of brood year on number of gill rakers in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	36.667	1.101	0.214	1.450	0.233
	6/22/56	6_3	30	36.200	2.717	0.301		
Do	6/16, 29/55	6_4	38	35.974	1.539	0.201	0.705	0.408
	6/22/56	6_4	53	36.189	1.386	0.162		
Do	6/22/56	5_3	15	36.600	2.114	0.375	0.230	0.629
	6/20/57	5_3	33	36.364	2.675	0.285		
Do	8/24/55	6_4	18	35.944	2.170	0.347	2.107	0.137
	9/7/56	6_4	68	36.412	2.007	0.172		
	8/21/57, 9/9, 17/57	6_4	58	36.724	2.238	0.196		
Do	9/7/56	5_3	16	36.438	2.526	0.397	0.472	0.494
	8/21/57, 9/9, 17/57	5_3	68	36.706	1.852	0.165		
Red River	6/18/55	6_3	17	37.176	1.156	0.261	2.262	0.112
	6/17, 18/56	6_3	40	36.475	1.691	0.205		
	6/21/57	6_3	46	36.826	1.257	0.165		
Do	6/18/56	5_3	31	36.806	1.760	0.238	0.832	0.368
	6/21/57	5_3	58	37.086	1.974	0.184		
Bristol Bay:								
Egegik weir	7/17/56	5_2	16	37.125	1.313	0.286	0.097	0.754
	7/13/57	5_2	15	37.267	1.921	0.358		
Do	7/17/56	5_3	16	37.188	2.026	0.356	0.090	0.760
	7/13/57	5_3	110	37.300	1.955	0.133		
Do	7/17/56	6_3	16	37.250	1.400	0.296	0.031	0.854
	7/13/57	6_3	106	37.189	1.735	0.128		
Ugashik weir	7/23/56	4_2	119	37.109	1.776	0.122	0.875	0.356
	7/19/57	4_2	30	37.367	1.965	0.256		
Do	7/23/56	5_3	34	36.765	1.700	0.224	0.380	0.537
	7/19/57	5_3	30	37.000	3.034	0.318		
Kvichak River	7/13/56	5_3	29	37.793	1.742	0.245	1.978	0.164
	7/10/57	5_3	52	37.346	1.956	0.194		

TABLE B 47. Effect of brood year on number of branchiostegal rays in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	13.958	0.302	0.112	3.676	0
	6/22/56	6_3	30	13.633	0.448	0.122		
Do	6/16, 29/55	6_4	38	13.790	0.495	0.114	[1]5.562	0
	6/22/56	6_4	55	13.436	0.509	0.096		
Do	6/22/56	5_3	15	13.733	0.350	0.153	0.635	0
	6/20/57	5_3	32	13.906	0.538	0.130		
Do	8/24/55	6_4	18	13.889	0.458	0.159	2.698	0
	9/7/56	6_4	68	13.647	0.560	0.090		
	8/21/57, 9/9, 17/57	6_4	58	13.931	0.450	0.088		
Do	9/7/56	5_3	16	13.875	0.513	0.179	0.327	0
	8/21/57, 9/9, 17/57	5_3	67	13.985	0.469	0.084		
Red River	6/18/55	6_3	17	14.118	0.362	0.146	2.031	0
	6/17, 18/56	6_3	40	14.000	0.564	0.119		
	6/21/57	6_3	46	14.304	0.483	0.102		
Do	6/18/56	5_3	31	14.387	0.446	0.120	0.086	0
	6/21/57	5_3	58	14.345	0.405	0.083		
Bristol Bay:								
Egegik weir	7/17/56	5_2	17	14.235	0.318	0.137	0.389	0
	7/13/57	5_2	15	14.400	0.828	0.235		
Do	7/17/56	5_3	16	14.063	0.460	0.169	3.472	0
	7/13/57	5_3	111	13.748	0.390	0.059		
Do	7/17/56	6_3	16	14.000	0.533	0.182	0.075	0
	7/13/57	6_3	105	13.943	0.612	0.076		
Ugashik weir	7/23/56	4_2	118	13.890	0.355	0.055	0.139	0
	7/19/57	4_2	30	13.933	0.203	0.082		
Do	7/23/56	5_3	29	13.828	0.575	0.141	1.384	0
	7/19/57	5_3	32	13.719	0.467	0.121		
Kvichak River	7/13/56	5_3	51	14.172	0.717	0.118	[1]6.717	0
	7/10/57	5_3	29	13.706	0.531	0.135		

[1] Significant at 5-percent level.

TABLE B–48. Effect of brood year on number of pectoral-fin rays in red salmon collected in 1955–57.

Area	Date	Age group	*N*	Mean	Variance	Standard error	*F*-value	*P*
Kodiak Island:								
Karluk weir	6/16, 29/55	6_3	24	16.167	0.231	0.098	[1]12.275	0.001
	6/22/56	6_3	30	16.633	0.241	0.089		
Do	6/16, 29/55	6_4	38	16.316	0.330	0.093	2.093	0.152
	6/22/56	6_4	55	16.491	0.328	0.077		
Do	6/22/56	5_3	15	16.533	0.264	0.133	0.377	0.542
	6/20/57	5_3	33	16.636	0.300	0.095		
Do	8/24/55	6_4	18	16.444	0.258	0.120	1.574	0.222
	9/7/56	6_4	69	16.551	0.398	0.075		
	8/21/57, 9/9, 17/57	6_4	58	16.690	0.287	0.070		
Do	9/7/56	5_3	16	16.625	0.246	0.124	1.586	0.211
	8/21/57, 9/9, 17/57	5_3	68	16.426	0.337	0.070		
Red River	6/18/55	6_3	16	16.412	0.381	0.154	1.714	0.191
	6/17, 18/56	6_3	40	16.425	0.353	0.094		
	6/21/57	6_3	46	16.630	0.282	0.078		
Do	6/18/56	5_3	31	16.581	0.316	0.101	0.053	0.817
	6/21/57	5_3	58	16.552	0.321	0.076		
Bristol Bay:								
Egegik weir	7/17/56	5_2	17	16.706	0.343	0.142	0.267	0.606
	7/13/57	5_2	15	16.800	0.171	0.108		
Do	7/17/56	5_3	16	16.750	0.333	0.144	3.134	0.083
	7/13/57	5_3	111	16.486	0.306	0.052		
Do	7/17/56	6_3	16	16.500	0.266	0.129	0.573	0.454
	7/13/57	6_3	106	16.396	0.260	0.049		
Ugashik weir	7/23/56	4_2	120	16.492	0.268	0.047	0.148	0.698
	7/19/57	4_2	30	16.533	0.327	0.104		
Do	7/23/56	5_3	34	16.471	0.256	0.087	3.424	0.070
	7/19/57	5_3	30	16.300	0.424	0.119		
Kvichak River	7/13/56	5_3	29	16.552	0.328	0.106	2.024	0.158
	7/10/57	5_3	52	16.365	0.314	0.077		

[1] Significant at 1-percent level.

TABLE B–49. Effect of brood year on number of dorsal-fin elements in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value
Kodiak Island:							
Karluk weir	6/16, 29/55	6_3	24	14.583	0.514	0.146	0.009
	6/22/56	6_3	30	14.600	0.317	0.102	
Do	6/16, 29/55	6_4	38	14.500	0.310	0.090	2.722
	6/22/56	6_4	55	14.709	0.395	0.084	
Do	6/22/56	5_3	15	14.600	0.257	0.131	1.277
	6/20/57	5_3	33	14.788	0.296	0.094	
Do	8/24/55	6_4	18	14.833	0.147	0.090	0.853
	9/7/56	6_4	68	14.647	0.410	0.077	
	8/21/57, 9/9, 17/57	6_4	58	14.638	0.305	0.072	
Do	9/7/56	5_3	16	14.375	0.246	0.124	[1]5.379
	8/21/57, 9/9, 17/57	5_3	68	14.765	0.391	0.075	
Red River	6/18/55	6_3	16	14.750	0.333	0.144	0.428
	6/17, 18/56	6_3	40	14.850	0.438	0.104	
	6/21/57	6_3	46	14.913	0.347	0.087	
Do	6/18/56	5_3	31	14.677	0.360	0.108	5.507
	6/21/57	5_3	58	14.983	0.333	0.075	
Bristol Bay:							
Egegik weir	7/17/56	5_2	17	14.824	0.406	0.154	3.048
	7/13/57	5_2	15	14.400	0.542	0.190	
Do	7/17/56	5_3	16	14.688	0.493	0.175	0.000
	7/13/57	5_3	111	14.684	0.308	0.052	
Do	7/17/56	6_3	16	14.500	0.266	0.129	[1]5.813
	7/13/57	6_3	106	14.858	0.313	0.054	
Ugashik weir	7/23/56	4_2	118	14.492	0.354	0.055	[1]5.411
	7/19/57	4_2	30	14.767	0.255	0.092	
Do	7/23/56	5_3	34	14.647	0.356	0.102	0.317
	7/19/57	5_3	30	14.900	0.231	0.088	
Kvichak River	7/13/56	5_3	28	14.714	0.285	0.100	1.312
	7/10/57	5_3	52	14.557	0.369	0.084	

[1] Significant at 5-percent level.

TABLE B–50. Effect of brood year on number of anal-fin elements in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
ak Island:								
Karluk weir	6/16, 29/55	6_3	24	18.000	0.521	0.147	0.869	0.361
	6/22/56	6_3	30	17.833	0.351	0.108		
Do	6/16, 29/55	6_4	38	17.947	0.321	0.092	0.093	0.759
	6/22/56	6_4	55	17.909	0.380	0.083		
Do	6/22/56	5_3	15	17.800	0.314	0.144	2.218	0.144
	6/20/57	5_3	32	18.063	0.319	0.099		
Do	8/24/55	6_4	18	17.944	0.170	0.097	0.383	0.707
	9/7/56	6_4	69	18.104	0.249	0.060		
	8/21/57, 9/9, 17/57	6_4	58	17.931	0.415	0.084		
Do	9/7/56	5_3	16	18.063	0.326	0.143	0.545	0.464
	8/21/57, 9/9, 17/57	5_3	68	17.941	0.355	0.072		
Red River	6/18/55	6_3	17	18.294	0.343	0.142	0.233	0.780
	6/17, 18/56	6_3	40	18.300	0.317	0.089		
	6/21/57	6_3	46	18.217	0.396	0.093		
Do	6/18/56	5_3	28	18.214	0.470	0.130	1.426	0.236
	6/21/57	5_3	57	18.386	0.348	0.078		
tol Bay:								
Egegik weir	7/17/56	5_2	17	17.765	0.318	0.137	0.022	0.878
	7/13/57	5_2	15	17.800	0.600	0.200		
Do	7/17/56	5_3	16	18.625	0.780	0.221	[1]16.800	<0.001
	7/13/57	5_3	110	17.909	0.376	0.058		
Do	7/17/56	6_3	16	18.000	0.666	0.204	0.013	0.911
	7/13/57	6_3	105	18.019	0.365	0.058		
Ugashik weir	7/23/56	4_2	119	17.908	0.254	0.046	2.356	0.128
	7/19/57	4_2	30	18.067	0.272	0.095		
Do	7/23/56	5_3	34	17.853	0.311	0.095	0.348	0.554
	7/19/57	5_3	30	17.933	0.341	0.106		
Kvichak River	7/13/56	5_3	27	18.148	0.515	0.138	1.869	0.176
	7/10/57	5_3	49	17.939	0.350	0.084		

ignificant at 1-percent level.

TABLE B–51. Effect of time of sampling on number of scales along the lateral line in red salmon collected in 1955–57

Area	Date	Age group	N	Mean	Variance	Standard error	F-value
1955:							
Kodiak Island:							
Karluk weir	6/16	6_4	15	130.000	4.143	0.525	1.349
	6/29	6_4	23	129.261	3.382	0.383	
1956:							
Kodiak Island:							
Red River	6/17	4_2	18	130.333	2.000	0.333	0.102
	6/18	4_2	52	130.519	3.118	0.245	
Bristol Bay:							
Naknek weir	7/6	5_2	28	130.750	5.081	0.426	0.243
	7/8	5_2	34	130.471	5.083	0.387	
Do	7/6	6_3	38	130.237	4.618	0.348	0.392
	7/8	6_3	39	129.897	6.673	0.414	
1957:							
Chignik:							
Chignik weir	7/26	5_2	18	132.111	3.400	0.435	2.859
	7/27	5_2	21	130.381	4.750	0.476	
	7/28	5_2	21	131.571	3.955	0.434	
Do	7/25	6_3	25	130.400	2.168	0.294	2.821
	7/27	6_3	28	131.071	2.811	0.317	
	7/28	6_3	22	131.455	2.738	0.354	
Kodiak Island:							
Karluk weir	8/21	5_3	14	130.429	2.108	0.388	0.445
	9/9	5_3	15	130.067	3.350	0.473	
	9/17	5_3	39	129.871	4.220	0.330	
Do	8/21	6_4	25	129.960	2.042	0.286	3.453
	9/17	6_4	20	130.850	3.184	0.399	
Bristol Bay:							
Naknek weir	7/3	5_2	38	129.868	4.873	0.359	0.411
	7/5	5_2	30	129.733	2.754	0.303	
	7/11	5_2	16	129.750	5.800	0.603	
	7/12	5_2	26	130.077	3.352	0.359	
	7/25	5_2	17	130.412	2.381	0.375	
Do	7/3	6_3	45	131.067	3.472	0.278	1.242
	7/5	6_3	62	130.500	3.565	0.240	
	7/11	6_3	35	130.371	2.416	0.263	
	7/12	6_3	48	131.271	5.903	0.352	
	7/21	6_3	39	130.769	5.708	0.384	
	7/25	6_3	75	131.107	5.745	0.277	
	7/29	6_3	20	131.300	5.273	0.514	
Kvichak River	7/9	5_2	53	131.000	2.692	0.225	0.386
	7/10	5_2	48	130.791	2.849	0.243	

TABLE B–52. Effect of time of sampling on number of scales below the lateral line in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
955:								
Kodiak Island:								
Karluk weir	6/16	6_4	15	20.333	2.093	0.373	1.098	0.304
	6/29	6_4	23	19.870	1.573	0.261		
956:								
Kodiak Island:								
Red River	6/17	4_2	18	20.778	1.477	0.286	0.401	0.527
	6/18	4_2	52	20.615	0.673	0.113		
Bristol Bay:								
Naknek weir	7/6	5_2	28	20.107	1.359	0.220	0.611	0.441
	7/8	5_2	34	19.882	1.197	0.187		
Do	7/6	6_3	38	20.184	0.964	0.159	0.647	0.428
	7/8	6_3	39	20.000	1.052	0.164		
957:								
Chignik:								
Chignik weir	7/26	5_2	18	21.555	1.200	0.258	[1]4.095	0.019
	7/27	5_2	21	20.714	0.815	0.196		
	7/28	5_2	21	20.810	0.960	0.213		
Do	7/25	6_3	25	21.080	0.908	0.190	0.701	0.520
	7/27	6_3	28	20.964	1.148	0.202		
	7/28	6_3	22	20.727	0.971	0.210		
Kodiak Island:								
Karluk weir	8/21	5_3	14	20.714	7.454	0.729	1.104	0.340
	9/9	5_3	15	20.333	0.950	0.251		
	9/17	5_3	38	19.973	1.648	0.208		
Do	8/21	6_4	26	19.923	0.792	0.174	0.928	0.345
	9/17	6_4	20	20.200	1.116	0.236		
Bristol Bay:								
Naknek weir	7/3	5_2	38	20.526	0.959	0.158	1.420	0.238
	7/5	5_2	30	20.200	0.786	0.161		
	7/11	5_2	16	20.625	0.513	0.178		
	7/12	5_2	26	20.538	1.060	0.201		
	7/25	5_2	17	20.824	0.656	0.196		
Do	7/3	6_3	45	19.822	0.876	0.139	0.775	0.607
	7/5	6_3	62	19.871	0.868	0.118		
	7/11	6_3	35	19.571	0.958	0.165		
	7/12	6_3	48	19.750	0.872	0.134		
	7/21	6_3	39	19.692	0.955	0.156		
	7/25	6_3	75	19.760	0.941	0.111		
	7/29	6_3	20	19.450	0.678	0.184		
Kvichak River	7/9	5_2	53	20.792	1.321	0.157	0.366	0.544
	7/10	5_2	48	20.666	0.780	0.127		

[1] Significant at 5-percent level.

TABLE B–53. Effect of time of sampling on number of vertebrae in red salmon collected in 1955–57.

Area	Date	Age group	*N*	Mean	Variance	Standard error	*F*-value	
1955:								
Kodiak Island:								
Karluk weir	6/16	6_4	15	67.000	0.857	0.238	0.086	0.
	6/29	6_4	23	67.087	0.718	0.176		
1956:								
Kodiak Island:								
Red River	6/17	4_2	18	67.167	0.500	0.166	0.087	0.
	6/18	4_2	51	67.176	0.548	0.103		
Bristol Bay:								
Naknek weir	7/6	5_2	27	67.407	0.942	0.186	0.009	0.
	7/8	5_2	34	67.382	1.031	0.174		
Do	7/6	6_3	37	67.378	1.297	0.187	0.015	0.
1957:								
Chignik:								
Chignik weir	7/26	5_2	18	67.778	0.653	0.190	1.160	0.
	7/27	5_2	21	67.333	0.935	0.210		
	7/28	5_2	20	67.450	0.995	0.222		
Do	7/25	6_3	25	67.160	0.642	0.160	0.564	0.
	7/27	6_3	26	67.115	0.588	0.150		
	7/28	6_3	20	67.350	0.553	0.166		
Kodiak Island:								
Karluk weir	9/9	5_3	14	67.214	1.108	0.281	0.063	0.
	9/17	5_3	39	67.282	0.629	0.126		
Do	8/21	6_4	25	67.360	0.575	0.151	1.527	0.
	9/17	6_4	20	67.650	0.658	0.181		
Bristol Bay:								
Naknek weir	7/3	5_2	37	67.135	0.841	0.150	0.048	0.
	7/5	5_2	28	66.893	0.617	0.148		
	7/11	5_2	15	66.933	0.921	0.247		
	7/12	5_2	24	67.083	0.947	0.198		
	7/25	5_2	17	67.176	0.656	0.196		
Do	7/3	6_3	43	67.581	0.773	0.133	1.431	0.
	7/5	6_3	59	67.305	0.698	0.108		
	7/11	6_3	34	67.324	0.710	0.144		
	7/12	6_3	44	67.682	1.245	0.531		
	7/21	6_3	38	67.658	1.258	0.575		
	7/25	6_3	72	67.611	1.198	0.407		
	7/29	6_3	19	67.842	0.805	0.205		
Kvichak River	7/9	5_2	52	67.403	0.598	0.107	0.715	0.
	7/10	5_2	48	67.270	0.627	0.114		

TABLE B–54. Effect of time of sampling on position of first haemal arch in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
1955:								
Kodiak Island:								
Karluk weir	6/16	6_4	15	34.867	0.693	0.215	0.407	0.525
	6/29	6_4	23	34.652	1.236	0.232		
1956:								
Kodiak Island:								
Red River	6/17	4_2	18	34.278	0.329	0.135	0.000	0.999
	6/18	4_2	51	34.275	0.604	0.109		
Bristol Bay:								
Naknek weir	7/6	5_2	26	34.654	0.636	0.156	0.087	0.767
	7/8	5_2	34	34.588	0.795	0.153		
Do	7/6	6_3	37	34.568	0.808	0.148	0.338	0.561
	7/8	6_3	38	34.447	0.794	0.145		
1957:								
Chignik:								
Chignik weir	7/26	5_2	18	35.056	0.406	0.150	[1]3.230	0.048
	7/27	5_2	21	34.905	0.690	0.181		
	7/28	5_2	20	34.500	0.368	0.136		
Do	7/25	6_3	25	34.240	1.192	0.218	1.003	0.330
	7/27	6_3	26	34.385	0.808	0.176		
	7/28	6_3	21	34.667	1.035	0.222		
Kodiak Island:								
Karluk weir	9/9	5_3	14	34.286	0.992	0.266	0.122	0.726
	9/17	5_3	39	34.384	0.769	0.140		
Do	8/21	6_4	25	34.480	0.842	0.183	1.431	0.237
	9/17	6_4	20	34.800	0.800	0.200		
Bristol Bay:								
Naknek weir	7/3	5_2	37	34.622	0.519	0.118	1.103	0.330
	7/5	5_2	29	34.241	0.689	0.154		
	7/11	5_2	15	34.267	0.778	0.228		
	7/12	5_2	24	34.292	0.913	0.195		
	7/25	5_2	17	34.412	0.756	0.211		
Do	7/3	6_3	45	34.667	1.045	0.152	1.277	0.290
	7/5	6_3	61	34.607	0.842	0.117		
	7/11	6_3	34	34.941	0.663	0.140		
	7/12	6_3	44	34.659	1.160	0.162		
	7/21	6_3	39	34.615	0.663	0.130		
	7/25	6_3	74	34.460	0.744	0.100		
	7/29	6_3	19	34.842	0.583	0.175		
Kvichak River	7/9	5_2	53	34.849	0.554	0.102	1.722	0.195
	7/10	5_2	48	34.645	0.659	0.117		

[1] Significant at 5-percent level.

TABLE B–55. Effect of time of sampling on number of ventral gill rakers in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	F
1955:								
Kodiak Island:								
Karluk weir	6/16	6_4	15	22.267	0.779	0.228	0.082	0.
	6/29	6_4	23	22.348	0.691	0.173		
1956:								
Kodiak Island:								
Red River	6/17	4_2	17	22.647	0.869	0.226	0.844	0.
	6/18	4_2	51	22.882	0.826	0.127		
Bristol Bay:								
Naknek weir	7/6	5_2	28	22.964	0.925	0.182	0.085	0.
	7/8	5_2	34	23.029	0.636	0.137		
Do	7/6	6_3	38	22.737	0.795	0.144	1.712	0.
	7/8	6_3	39	23.026	1.078	0.166		
1957:								
Chignik:								
Chignik weir	7/26	5_2	18	23.444	0.377	0.144	0.308	0.
	7/27	5_2	21	23.476	0.760	0.190		
	7/28	5_2	21	23.286	0.915	0.208		
Do	7/25	6_3	25	23.200	0.833	0.182	0.400	0.
	7/27	6_3	28	23.143	0.718	0.160		
	7/28	6_3	22	23.364	0.814	0.192		
Kodiak Island:								
Karluk weir	8/21	5_3	14	22.571	0.415	0.172	0.979	0.
	9/9	5_3	15	23.000	0.571	0.195		
	9/17	5_3	39	22.717	0.892	0.151		
Do	8/21	6_4	26	22.846	1.016	0.197	0.107	0.
	9/17	6_4	20	22.750	0.932	0.216		
Bristol Bay:								
Naknek weir	7/3	5_2	37	22.784	0.619	0.129	0.973	0.
	7/5	5_2	29	22.828	1.005	0.186		
	7/11	5_2	16	22.438	2.127	0.365		
	7/12	5_2	26	23.000	0.560	0.147		
	7/25	5_2	17	22.941	0.681	0.200		
Do	7/3	6_3	45	23.089	0.719	0.126	1.300	0.
	7/5	6_3	61	22.836	0.639	0.102		
	7/11	6_3	35	22.886	0.634	0.134		
	7/12	6_3	48	23.188	1.092	0.145		
	7/21	6_3	39	23.180	0.888	0.151		
	7/25	6_3	74	23.176	0.887	0.109		
	7/29	6_3	20	23.100	1.147	0.239		
Kvichak River	7/9	5_2	53	23.113	0.602	0.106	0.196	0.
	7/10	5_2	48	23.041	0.721	0.122		

TABLE B–56. Effect of time of sampling on number of gill rakers in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
55:								
Kodiak Island:								
Karluk weir	6/16	6_4	15	35.667	1.521	0.318	1.537	0.222
	6/29	6_4	23	36.174	1.514	0.256		
56:								
Kodiak Island:								
Red River	6/17	4_2	17	37.059	1.681	0.314	0.007	0.939
	6/18	4_2	51	37.098	1.490	0.170		
Bristol Bay:								
Naknek weir	7/6	5_2	28	37.143	1.904	0.260	0.000	0.999
	7/8	5_2	34	37.147	1.038	0.174		
Do	7/6	6_3	38	36.711	1.562	0.202	2.578	0.113
	7/8	6_3	39	37.231	2.498	0.252		
957:								
Chignik:								
Chignik weir	7/26	5_2	18	37.611	1.312	0.269	0.187	0.833
	7/27	5_2	21	37.810	2.560	0.349		
	7/28	5_2	21	37.571	1.456	0.263		
Do	7/25	6_3	25	37.400	1.750	0.264	0.000	0.999
	7/27	6_3	28	37.393	1.730	0.248		
	7/28	6_3	22	37.409	1.871	0.291		
Kodiak Island:								
Karluk weir	8/21	5_3	14	36.071	0.992	0.266	2.961	0.054
	9/9	5_3	15	37.267	1.779	0.358		
	9/17	5_3	39	36.717	1.997	0.226		
Do	8/21	6_4	26	36.731	2.524	0.311	0.079	0.777
	9/17	6_4	20	36.600	2.147	0.328		
Bristol Bay:								
Naknek weir	7/3	5_2	37	36.568	1.253	0.184	0.566	0.690
	7/5	5_2	29	36.690	2.365	0.285		
	7/11	5_2	16	36.313	4.093	0.506		
	7/12	5_2	26	36.923	0.952	0.191		
	7/25	5_2	17	36.765	1.819	0.327		
Do	7/3	6_3	45	37.400	1.518	0.183	1.121	0.345
	7/5	6_3	61	37.115	1.637	0.164		
	7/11	6_3	35	37.057	1.173	0.183		
	7/12	6_3	48	37.625	2.027	0.205		
	7/21	6_3	39	37.308	1.745	0.211		
	7/25	6_3	74	37.466	1.622	0.148		
	7/29	6_3	20	37.300	1.800	0.300		
Kvichak River	7/9	5_2	53	37.396	1.475	0.167	0.455	0.501
	7/10	5_2	48	37.229	1.712	0.189		

TABLE B–57. Effect of time of sampling on number of branchiostegal rays in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value
1955:							
Kodiak Island:							
Karluk weir	6/16	6_4	15	13.600	0.686	0.214	1.840
	6/29	6_4	23	13.913	0.355	0.122	
1956:							
Kodiak Island:							
Red River	6/17	4_2	18	14.333	0.353	0.141	0.660
	6/18	4_2	52	14.173	0.577	0.105	
Bristol Bay:							
Naknek weir	7/6	5_2	28	13.607	0.619	0.149	1.118
	7/8	5_2	33	13.424	0.314	0.308	
Do	7/6	6_3	38	13.553	0.524	0.117	0.054
	7/8	6_3	39	13.590	0.459	0.109	
1957:							
Chignik:							
Chignik weir	7/26	5_2	18	14.389	0.846	0.217	0.311
	7/27	5_2	20	14.600	0.768	0.196	
	7/28	5_2	21	14.429	0.721	0.185	
Do	7/25	6_3	24	14.708	0.391	0.126	2.783
	7/27	6_3	28	14.464	0.481	0.130	
	7/28	6_3	22	14.227	0.567	0.161	
Kodiak Island:							
Karluk weir	9/9	5_3	15	13.933	0.493	0.182	0.219
	9/17	5_3	39	14.025	0.394	0.100	
Do	8/21	6_4	26	13.846	0.536	0.141	0.238
	9/17	6_4	20	13.950	0.468	0.153	
Bristol Bay:							
Naknek weir	7/3	5_2	37	13.838	0.417	0.105	0.950
	7/5	5_2	30	13.700	0.424	0.119	
	7/11	5_2	16	14.063	0.593	0.192	
	7/12	5_2	26	13.885	0.508	0.140	
	7/25	5_2	17	14.000	0.500	0.171	
Do	7/3	6_3	44	13.727	0.529	0.110	0.785
	7/5	6_3	61	13.623	0.439	0.084	
	7/11	6_3	35	13.629	0.419	0.109	
	7/12	6_3	48	13.812	0.666	0.117	
	7/21	6_3	40	13.700	0.472	0.109	
	7/25	6_3	73	13.548	0.529	0.085	
	7/29	6_3	20	13.650	0.553	0.166	
Kvichak River	7/9	5_2	52	13.884	0.535	0.101	0.074
	7/10	5_2	47	13.872	0.462	0.099	

TABLE B–58. Effect of time of sampling on number of pectoral-fin rays in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
55:								
Kodiak Island:								
Karluk weir	6/16	6_4	15	16.333	0.521	0.186	0.022	0.874
	6/29	6_4	23	16.304	0.223	0.097		
56:								
Kodiak Island:								
Red River	6/17	4_2	18	16.500	0.265	0.121	0.252	0.614
	6/18	4_2	52	16.423	0.328	0.079		
Bristol Bay:								
Naknek weir	7/6	5_2	28	16.214	0.322	0.107	0.003	0.983
	7/8	5_2	34	16.206	0.350	0.100		
Do	7/6	6_3	38	16.211	0.278	0.085	0.384	0.586
	7/8	6_3	38	16.316	0.817	0.146		
957:								
Chignik:								
Chignik weir	7/26	5_2	18	16.222	0.300	0.128	1.404	0.257
	7/27	5_2	21	16.286	0.315	0.122		
	7/28	5_2	21	16.524	0.460	0.147		
Do	7/25	6_3	25	16.520	0.342	0.116	2.513	0.057
	7/27	6_3	28	16.214	0.248	0.093		
	7/28	6_3	22	16.273	0.210	0.097		
Kodiak Island:								
Karluk weir	8/21	5_3	14	16.357	0.246	0.132	0.497	0.620
	9/9	5_3	15	16.333	0.521	0.186		
	9/17	5_3	39	16.487	0.309	0.088		
Do	8/21	6_4	26	16.692	0.300	0.107	0.002	0.993
	9/17	6_4	20	16.700	0.326	0.127		
Bristol Bay:								
Naknek weir	7/3	5_2	38	16.263	0.308	0.090	1.710	0.115
	7/5	5_2	30	16.367	0.240	0.089		
	7/11	5_2	16	16.625	0.247	0.124		
	7/12	5_2	26	16.192	0.400	0.123		
	7/25	5_2	17	16.294	0.344	0.142		
Do	7/3	6_3	45	16.244	0.325	0.084	1.278	0.270
	7/5	6_3	62	16.371	0.368	0.076		
	7/11	6_3	35	16.057	0.468	0.115		
	7/12	6_3	48	16.312	0.390	0.090		
	7/21	6_3	40	16.225	0.333	0.091		
	7/25	6_3	75	16.253	0.327	0.065		
	7/29	6_3	20	16.400	0.358	0.133		
Kvichak River	7/9	5_2	53	16.641	0.350	0.081	0.515	0.475
	7/10	5_2	48	16.562	0.251	0.072		

TABLE B–59. Effect of time of sampling on number of dorsal-fin elements in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value
1955:							
Kodiak Island:							
Karluk weir	6/16	6_4	15	14.533	0.407	0.164	0.086
	6/29	6_4	23	14.478	0.259	0.105	
1956:							
Kodiak Island:							
Red River	6/17	4_2	18	14.778	0.300	0.128	[1]9.172
	6/18	4_2	52	14.211	0.523	0.100	
Bristol Bay:							
Naknek weir	7/6	5_2	28	14.500	0.482	0.131	0.116
	7/8	5_2	34	14.559	0.436	0.113	
Do	7/6	6_3	38	14.684	0.276	0.084	1.184
	7/8	6_3	39	14.538	0.413	0.102	
1957:							
Chignik:							
Chignik weir	7/26	5_2	18	14.556	0.494	0.165	1.514
	7/27	5_2	20	14.506	0.368	0.135	
	7/28	5_2	21	14.810	0.260	0.110	
Do	7/25	6_3	25	14.760	0.275	0.104	0.018
	7/27	6_3	27	14.741	0.277	0.100	
	7/28	6_3	22	14.727	0.400	0.134	
Kodiak Island:							
Karluk weir	8/21	5_3	14	15.000	0.308	0.148	2.009
	9/9	5_3	15	14.867	0.264	0.132	
	9/17	5_3	39	14.641	0.447	0.106	
Do	8/21	6_4	26	14.538	0.520	0.126	0.409
	9/17	6_4	20	14.650	0.237	0.108	
Bristol Bay:							
Naknek weir	7/3	5_2	38	14.711	0.427	0.105	0.455
	7/5	5_2	30	14.800	0.372	0.111	
	7/11	5_2	16	14.625	0.247	0.124	
	7/12	5_2	26	14.538	0.260	0.100	
	7/25	5_2	17	14.824	0.156	0.095	
Do	7/3	6_3	45	14.978	0.340	0.086	1.406
	7/5	6_3	62	14.774	0.374	0.077	
	7/11	6_3	35	14.600	0.247	0.083	
	7/12	6_3	48	14.812	0.368	0.087	
	7/21	6_3	40	14.800	0.523	0.114	
	7/25	6_3	75	14.760	0.347	0.067	
	7/29	6_3	20	14.850	0.237	0.108	
Kvichak River	7/9	5_2	53	14.754	0.304	0.075	0.392
	7/10	5_2	47	14.829	0.405	0.092	

[1] Significant at 1-percent level.

TABLE B–60. Effect of time of sampling on number of anal-fin elements in red salmon collected in 1955–57.

Area	Date	Age group	N	Mean	Variance	Standard error	F-value	P
5:								
Kodiak Island:								
Karluk weir	6/16	6_4	15	17.933	0.207	0.117	0.014	0.901
	6/29	6_4	23	17.957	0.409	0.133		
6:								
Kodiak Island:								
Red River	6/17	4_2	18	18.056	0.406	0.150	0.054	0.813
	6/18	4_2	52	18.096	0.402	0.087		
Bristol Bay:								
Naknek weir	7/6	5_2	27	17.963	0.500	0.136	0.058	0.806
	7/8	5_2	34	18.000	0.242	0.084		
Do	7/6	6_3	38	17.816	0.316	0.091	0.807	0.376
	7/8	6_3	39	17.949	0.524	0.116		
57:								
Chignik:								
Chignik weir	7/26	5_2	18	18.278	0.329	0.135	17.072	0.005
	7/27	5_2	21	17.762	0.390	0.136		
	7/28	5_2	21	18.429	0.355	0.130		
Do	7/25	6_3	25	18.280	0.375	0.122	0.108	0.898
	7/27	6_3	28	18.036	0.407	0.120		
	7/28	6_3	22	18.091	0.371	0.130		
Kodiak Island:								
Karluk weir	8/21	5_3	14	18.143	0.285	0.142	1.385	0.266
	9/9	5_3	15	18.000	0.286	0.138		
	9/17	5_3	39	17.846	0.397	0.100		
Do	8/21	6_4	26	17.885	0.508	0.140	0.352	0.553
	9/17	6_4	20	18.000	0.316	0.126		
Bristol Bay:								
Naknek weir	7/3	5_2	37	17.919	0.356	0.098	0.781	0.581
	7/5	5_2	30	17.833	0.557	0.136		
	7/11	5_2	16	17.938	0.460	0.169		
	7/12	5_2	26	18.077	0.392	0.122		
	7/25	5_2	17	18.118	0.363	0.146		
Do	7/3	6_3	45	18.089	0.674	0.122	0.324	0.940
	7/5	6_3	62	18.048	0.375	0.077		
	7/11	6_3	35	17.914	0.434	0.111		
	7/12	6_3	48	18.042	0.338	0.083		
	7/21	6_3	40	18.025	0.692	0.132		
	7/25	6_3	15	18.013	0.581	0.197		
	7/29	6_3	19	18.158	0.361	0.138		
Kvichak River	7/9	5_2	53	17.905	0.241	0.167	4.037	0.051
	7/10	5_2	48	18.125	0.324	0.082		

[1] Significant at 1-percent level.

APPENDIX C. COMPUTATIONAL STAGES FOR OBTAINING SUCCESSIVE DISCRIMINANT FUNCTIONS (Y_i) AND D_i^2 VALUES.

DISPERSION MATRIX

X_1	X_2	X_3	X_4	X_5	X_6	X_7	Difference (D
3.796657	1.169526	0.558848	0.148560	0.282691	0.061674	0.177691	1.05288
	0.774348	0.329565	0.037967	0.069959	0.020371	0.085767	0.21557
		0.700506	-0.007983	0.008188	0.021334	0.014182	0.35652
			0.921983	1.168426	0.034825	0.028233	0.70161
				2.007370	0.068321	0.051723	1.42923
					0.338930	0.021010	0.59614
						0.395240	0.07221
							0.00000
1.000000	0.308040	0.147195	0.039129	0.074458	0.016244	0.046802	0.27731
0.308040	0.414087	0.157417	-0.007795	-0.017121	0.001373	0.031031	-0.10875
0.147195		0.618246	-0.029850	-0.033423	0.012256	-0.011973	0.20154
0.039129			0.916170	1.157365	0.032412	0.021280	0.66041
0.074458				1.986321	0.063729	0.038492	1.35083
0.016244					0.337928	0.018124	0.57904
0.046802						0.386924	0.02294
Y_1=0.277318							-0.29198
0.743902	1.000000	0.380154	-0.018825	-0.041346	0.003316	0.074938	-0.26263
0.030092	0.380154	0.558403	-0.026887	-0.026914	0.011734	-0.023770	0.24288
0.044928	-0.018825		0.916023	1.157043	0.032438	0.021864	0.65837
0.087194	-0.041346			1.985613	0.063786	0.039775	1.34633
0.015223	0.003316				0.337923	0.018021	0.57940
0.023718	0.074938					0.384599	0.03109
Y_2=0.358220	-0.262636						-0.32054
0.053889	0.680788	1.000000	-0.048150	-0.048198	0.021013	-0.042568	0.43496
0.046377	-0.000521	-0.048150	0.914728	1.155747	0.033003	0.020719	0.67006
0.088644	-0.023023	-0.048198		1.984316	0.064352	0.038629	1.35804
0.014591	-0.004672	0.021013			0.337676	0.018521	0.57429
0.024999	0.091120	-0.042568				0.383587	0.04143
Y_3=0.345131	-0.427990	0.434965					-0.42619
0.050700	-0.000570	-0.052639	1.000000	1.263487	0.036080	0.022650	0.73253
0.030047	-0.022365	0.012639	1.263487	0.524045	0.022653	0.012451	0.51142
0.012918	-0.004653	0.022750	0.036080		0.336485	0.017772	0.55012
0.023949	0.091132	-0.041477	0.022650			0.383118	0.02625
Y_4=0.311158	-0.427608	0.470236	0.732531				-0.91703
0.057337	-0.042678	0.024118	2.411028	1.000000	0.043227	0.023759	0.97591
0.011619	-0.003686	0.022204	-0.018537	0.043227	0.335506	0.017234	0.52801
0.023235	0.091663	-0.041777	-0.007369	0.023759		0.382822	0.01410
Y_5=0.281835	-0.405781	0.457901	-0.500529	0.975918			-1.41614
0.034631	-0.010986	0.066181	-0.055251	0.128841	1.000000	0.051367	1.57338
0.022638	0.091852	-0.042918	-0.006417	0.021539	0.051367	0.381937	-0.01302
Y_6=0.263549	-0.399980	0.422957	-0.471356	0.907888	1.573787		-2.24713
0.059272	0.240490	-0.112369	-0.016801	0.056394	0.134491	1.000000	-0.03408
Y_7=0.264321	-0.396849	0.421494	-0.471575	0.908622	1.575538	-0.034089	-2.24757

SUMMARY

The discriminant function (using seven characters) is—

$$Y = 0.264321\ X_1 - 0.396849\ X_2 + 0.421494\ X_3 - 0.471575\ X_4 + 0.908622\ X_5 + 1.575538\ X_6 - 0.034089\ X_7$$

$D^2 = 2.247574$; hence, the probability of correct classification=0.7734 (or 77.34%)

$\overline{Y}_a = 70.4319$ (for western Alaska)

$\overline{Y}_b = 68.1843$ (for Okhotsk Sea)

$Y_0 = 1/2\ (\overline{Y}_a + \overline{Y}_b) = 69.308$ (critical value)

APPENDIX D. DISTRIBUTION OF SEVEN MORPHOLOGICAL CHARACTERS FOR RED SALMON FROM NORTH AMERICAN AND ASIAN REFERENCE AREAS

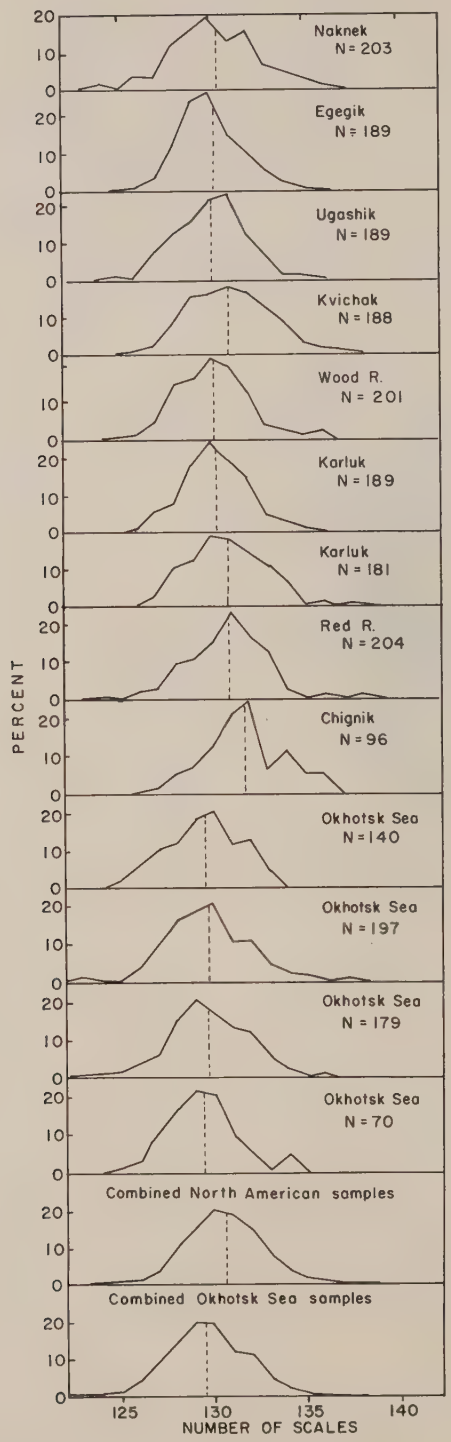

FIGURE D–1. Percentage frequency distribution of number of scales along the lateral line in red salmon from North American and Asian area standards. (Broken lines show position of mean.)

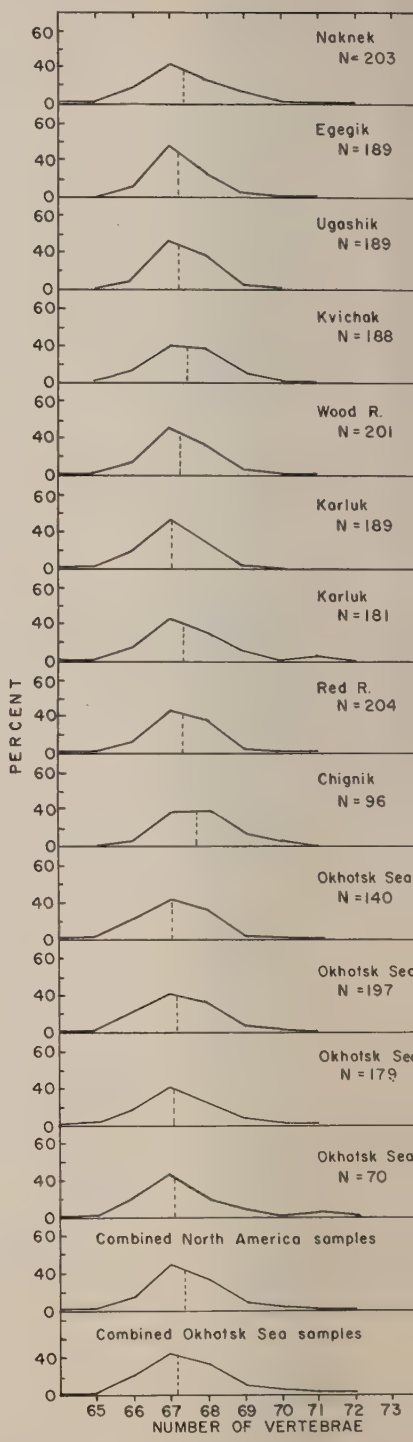

FIGURE D–2. Percentage frequency distribution of number of vertebrae in red salmon from North Am and Asian area standards. (Broken lines show p of mean.)

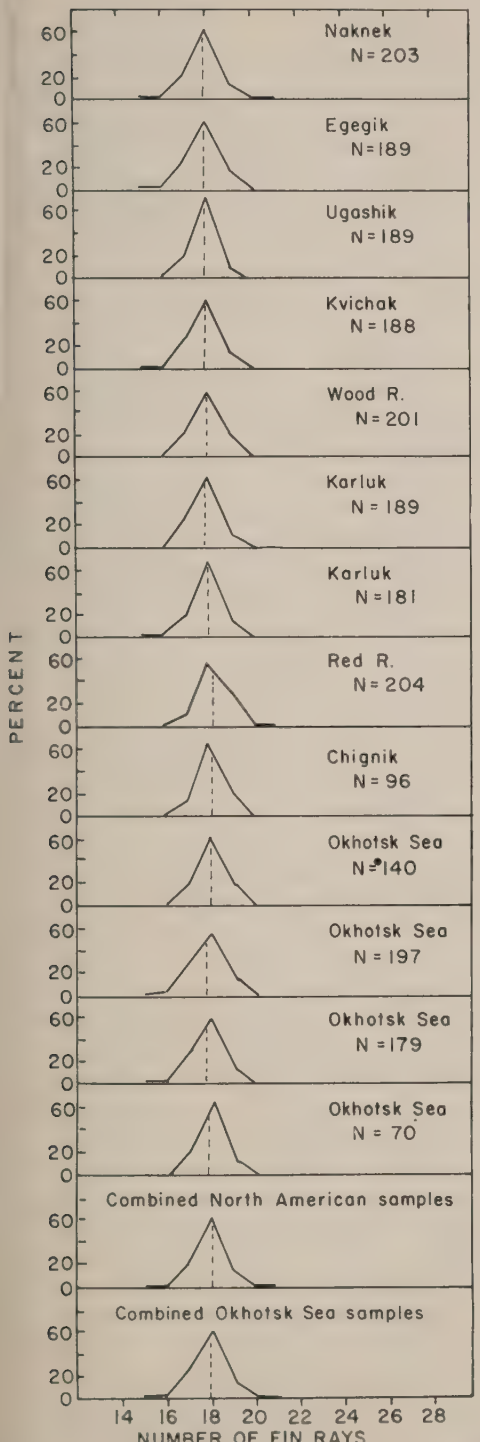

FIGURE D–3. Percentage frequency distribution of ~~position of first haemal arch~~ number of anal fin rays in red salmon from North American and Asian area standards. (Broken lines show position of mean.)

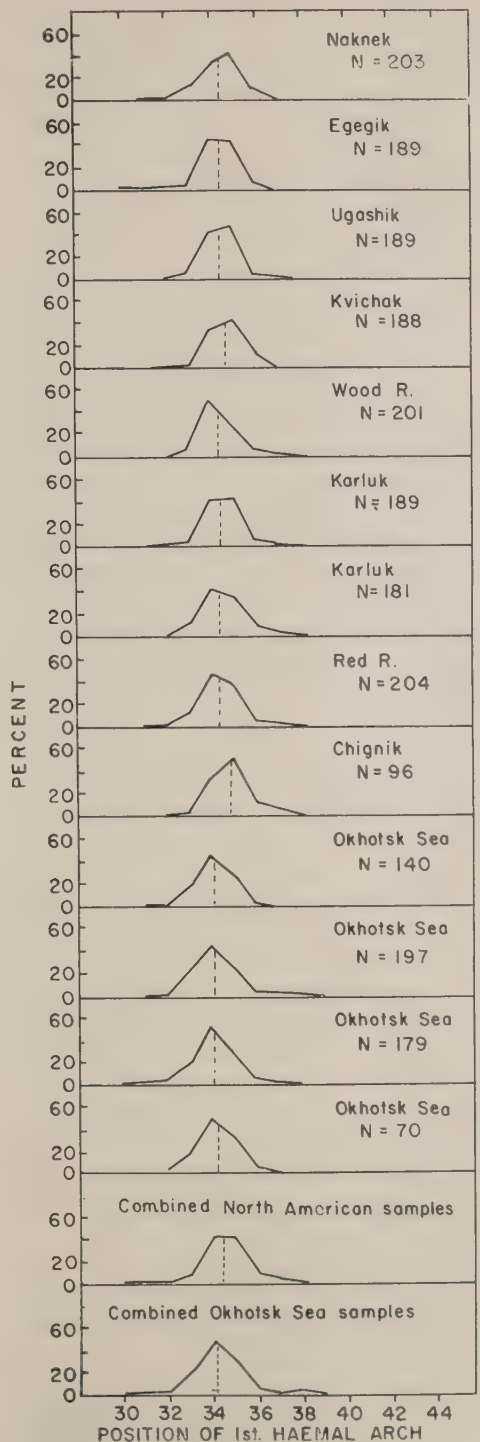

FIGURE D–4. Percentage frequency distribution of ~~number~~ position of first haemal arch of ventral gill rakers in red salmon from North American and Asian area standards. (Broken lines show position of mean.)

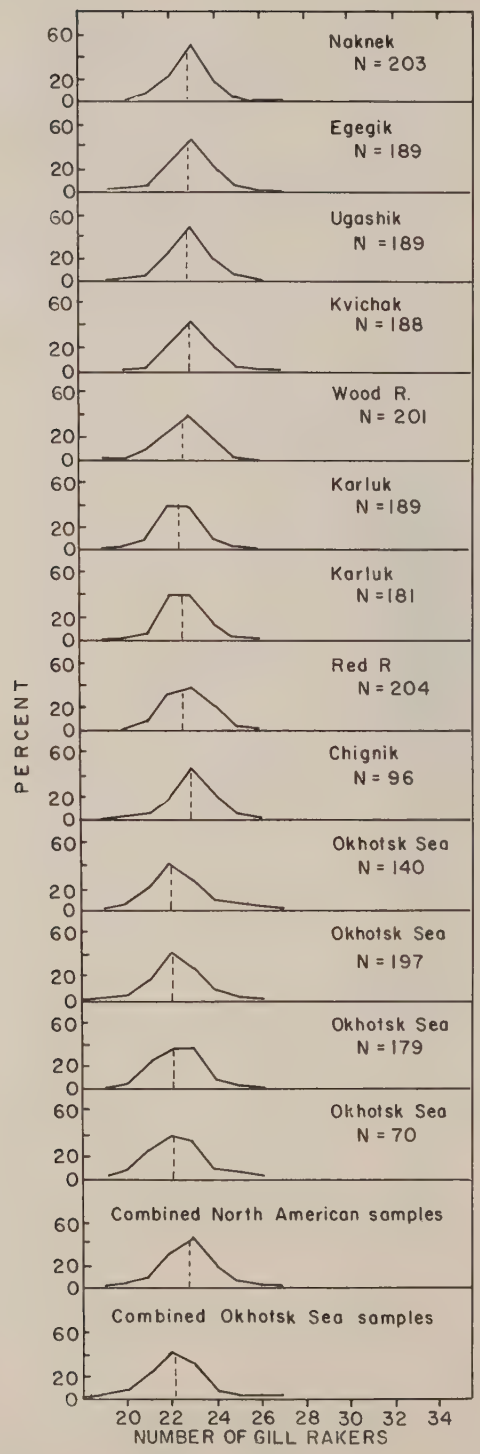

FIGURE D-5. Percentage frequency distribution of number of gill rakers in red salmon from North American and Asian area standards. (Broken lines show position of mean.)

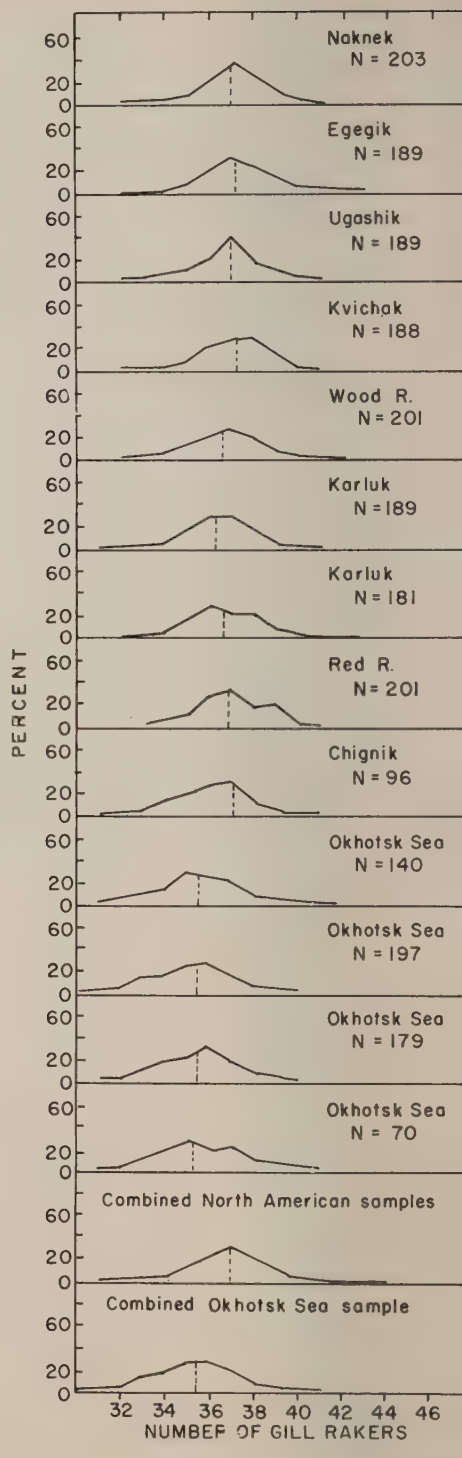

FIGURE D-6. Percentage frequency distribution of number of gill rakers in red salmon from North American and Asian area standards. (Broken lines show position of mean.)

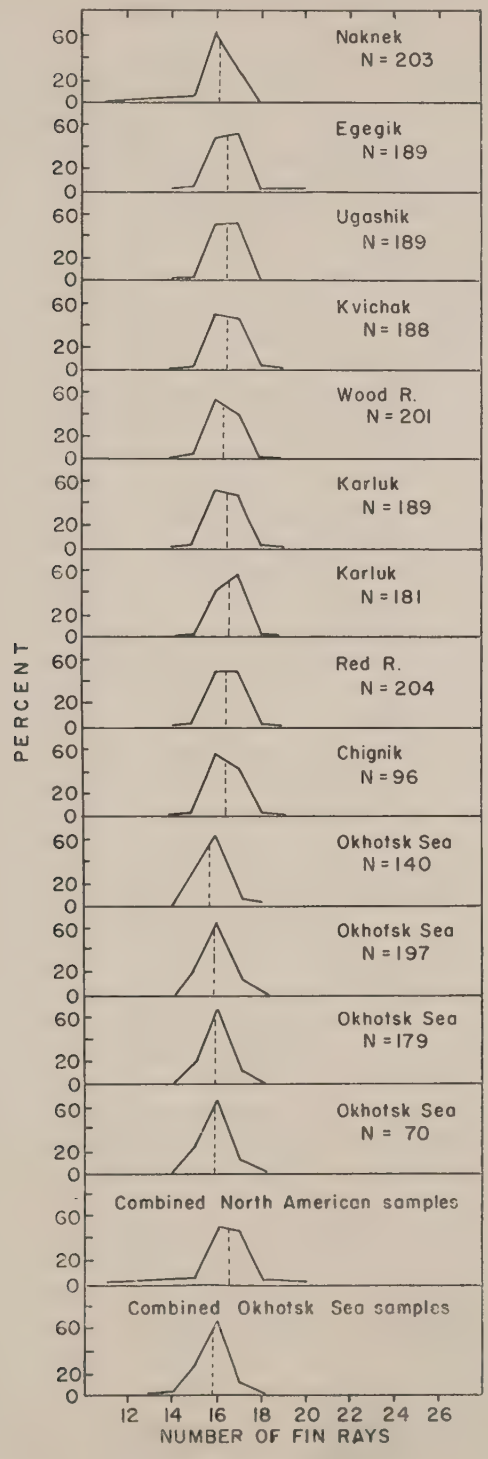

FIGURE D 7.—Percentage frequency distribution of number of pectoral fin rays in red salmon from North American and Asian area standards. (Broken lines show position of mean.)

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NOTES ON SHELL MORPHOLOGY, GROWTH, AND DISTRIBUTION OF *OSTREA EQUESTRIS* SAY

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ABSTRACT

The range of distribution of *Ostrea equestris* was found to extend north as far as 37°31′N, about half-way between Delaware and Chesapeake Bays. This species prefers water of high salinity; it is frequently found on ship wrecks off North Carolina islands and inside the stabilizer tubes of navigation buoys. Variations in shell morphology, denticulation, and size were studied in a population of *O. equestris* found growing in the sheltered environment inside the stabilizer tube of the buoy off the entrance to St. Mary's River (S. C.). The population comprised two successive year classes. The described variations were found to be associated with the crowding and could not be attributed to physical and chemical factors of the environment. The largest specimen measured 82 mm in height.

INTRODUCTION

Ostrea equestris is a small, economically unimportant bivalve of e Atlantic and Gulf Coasts and West Indies. In several locations ong the coast of the United States this hermaphroditic and larvi-arous oyster is found together with *Crassostrea virginica* and *Ostrea ons*. The northern boundary of its distribution has been reported be Cape Hatteras, North Carolina (Smith, 1937). Southward the ecies extends to the Gulf States and West Indies. Abbott (1954) marks that *O. equestris* lives in waters of greater salinity than that und over the bottoms occupied by *C. virginica*.

Pearse and Wharton (1938) mention the occurrence of *O. eques-is* throughout Apalachicola Bay, Florida. The presence of *O. eques-is* in this body of water will probably vary depending mainly on evailing salinities which change from year to year. Dr. R. W. enzel states (personal communication) that *O. equestris* in the astal waters of the Gulf is found in the subtidal regions in salinities ove 20-25‰.

In the offshore areas it thrives in highly saline waters. Wells and ray (1960) found *O. equestris* growing in great abundance on the ecks of ships on the ocean side of the chain of islands in the vicinity Cape Hatteras, North Carolina, where the salinity is about 35‰. ere, *O. equestris* far outnumbered *C. virginica*. In the Port Aransas

area, Texas, where *C. virginica* and *O. equestris* live together, annual range of salinity is from 33 to 38‰ (Menzel, 1955). The of *O. equestris* is here more numerous near the bottom, whereas of *C. virginica* sets predominantly near the surface.

O. equestris does not form beds or reefs but sometimes outnum *C. virginica* in the oyster beds below low tide level (some Flo bays) and on rock jetties adjacent to Beaufort Inlet, North Carol (personal communication of Dr. Harry W. Wells). Parker (19 finds that this "high salinity" species of oyster replaces *C. virgi* when the concentration of salts rise above 30‰ and that du droughts *O. equestris* "may completely replace *C. virginica* on low salinity reefs."

To persons unacquainted with the diagnostic characters of species, *O. equestris* may appear as a young seed oyster of *C. virgin* On several occasions this error was observed by one of us w examining barges with seed oysters gathered for replanting depl oyster grounds. The load consisted predominantly of *O. equestri*

Records on file in the Bureau of Commercial Fisheries show tha 1944 an attempt to transplant *O. equestris* to the Pacific Coast made by the State of Oregon, presumably in connection with an oy culture program of the State. The results of this undertaking are known.

Description of the Species

The original description of *O. equestris* by Say (1834) lists following characters:

> Shell small, with transverse wrinkles, and more or less deeply and angu folded longitudinally; ovate-triangular, tinted with violaceous; lateral ma near the hinge with from six to twelve denticulations of the superior v received into corresponding cavities of the inferior valve; superior v depressed but slightly folded; inferior valve convex, attached by a po of its surface, the margins elevated, folds unequal, much more profound those of superior valve; hinge very narrow, and curved laterally and ruptly.

Say adds that the most remarkable feature of the shell of *O. eq tris* is the "very abrupt lateral curvature of the beak, the continued of which may be traced in favourable specimens on the exterior inferior part of the umbo." Lamy (1929) mentions only the ra folds of the lower valve and the denticles near the hinge region as distinguishing characters of the species. He repeats Hanley's (18 admission that *O. equestris* may be a juvenile form of *Ostrea fron*

In an abbreviated form and with some variations, the diagnosi

. *equestris* given by Say appears in recent books on American shells. ometimes the presence of a series of denticles is omitted from the agnosis, although these structures seem to be a persistent character f the species.

Our synonymy of *O. equestris,* based on a review of the original escriptions and on opinions of others in recent years follows.

Ostrea equestris Say

Ostrea equestris Say, 1834, American Conchology, pl. 58; Binney, W. G., 1858, The complete writings of Thomas Say on the Conchology of the United States, p. 218, pl. 58.
Ostrea spreta Orbigny, 1846, Voyage Amerique Meridionale (Moll), p. 672.
Ostrea gundata Holmes, 1858-1860, Post-pleiocene fossils of South Carolina, *11*: pl. 2, fig. 10.
Ostrea cristata "Born" McLean, 1941, Notulae Naturae, Acad. Nat. Sci. Philadelphia, No. 67, p. 6; McLean, 1951, (*non* Born, 1778).

The most significant combination of features which distinguishes *O. equestris* from other species is, in our opinion, a rather high, ertical and crenulated margin of the lower valve; slightly off-center osition of the adductor muscle scar; a dull greenish undertone in the nterior surface; and the presence of a single row of denticles along

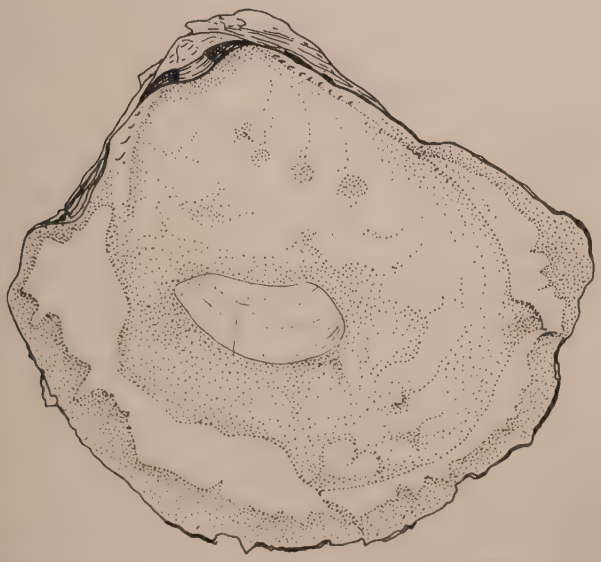


FIGURE 1. Inner side of the upper (right) valve of *Ostrea equestris.*

the lateral margin of the upper valve with the corresponding dep sions on the lower valve (Fig. 1). As in many other species Ostreidae the shape of *O. equestris* varies depending on crowding a the type of substratum upon which the oyster grows.

Two other species of the genus *Ostrea, O. frons* and *O. perm* occur in the Gulf of Mexico and the West Indies. The shells of *frons* have the following characters which distinguish them from ot species: radial plicate sculpture and sharply folded valve marg muscle scar close to the hinge; minute pimples along the entire circu ference of the valves; translucent white interior side of the shell a usually purplish red exterior. Hook-like projections for attachmen stems and branches of mangrove trees are frequently present. T may be absent from the oyster growing on a flat surface (Gun 1951) while in some specimens only remnants of hooks develop n the hinge. We have always noticed, however, at least some vestige hooks on specimens attached to flat surfaces on off-shore navigat buoys.

Ostrea permollis Sowerby lives as a commensal in sponges. I usually found completely embedded in sponge tissue with only margins of the valves visible on the surface. Specimens in our col tion from the northeast corner of the Gulf of Mexico, off the Flor coast, are embedded in *Stelleta grubii* (Schmidt). Besides the co mensal mode of existence the species is characterized by well develo beaks twisted back; the valves are light orange to fawn on the ou surface and white inside, with soft, silky epidermis. The inner marg of the valves bear numerous small and round denticles. The roun muscle scar is subcentral.

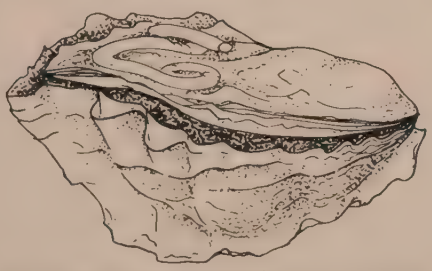
An opportunity to examine the extent of variability within a sin population of *O. equestris* grown in an unusual environment occur in the course of systematic studies conducted on fouling of navigat buoys (Merrill, 1961). The navigation buoys used by the U.S. Co Guard in open ocean waters are made up of a large cylindrical fl chamber which supports the superstructure consisting of a framew to which a light, and a bell or whistle are attached. Usually an op tube of large diameter extends below the float chamber and functi as a stabilizer. A small hole in the upper end of the stabilizer allo for the escape of air. Thus, the stabilizer tube helps the buoy maintain a vertical position and at the same time allows for a free, gradual exchange of water within the tube as the buoy surges up a down. The inside of the tube is dark; the animals that settle wit

e sheltered from violent currents and wave action and are well otected against attacks of many enemies.

The buoy in which large numbers of *O. equestris* were found was cated over a depth of 30 feet in the ocean (30°42′5″N, 81°19′2″W) pposite the entrance to St. Mary's River about 6 miles from the earest land point of Amelia Island and 7 miles from Cumberland land. It remained in the water from February 28, 1957, to Novem- er 16, 1960, when it was brought to the Coast Guard Base and xamined. Careful examination of the buoy before any material was emoved showed that *O. equestris* was the predominant fouling animal. was overgrowing the barnacles which obviously were the first ones settle inside the tube. Approximately 50 square feet of the inner rface of the stabilizer were covered by *O. equestris* of different sizes nd shapes. Small oysters of the species were attached to the buoy rface and to the valves of larger oysters; they comprised 25 percent f the 820 individuals. The density of the population attached directly the inner surface of the tube averaged 12 per square foot. This epresents an uncrowded condition. There were no oysters growing n the outside surface of the stabilizer or float.

Upon removal from the buoys the oysters were separated, measured, nd their shells examined. It was apparent from a study of the entire eries that the shape of the shell is greatly influenced by the degree f crowding.

If the growth of *O. equestris* is not obstructed by the irregularities f the substratum or by crowding, the shell becomes almost round Fig. 1), its height being almost equal or slightly less than the length ratio 1 or smaller). In the majority of the oysters in our sample the L ratio varied from 1.0 to 1.5. Two extremely high shells were ound in which the ratio was 2.02 and 2.08. Oysters growing in



IGURE 2. Side view of *Ostrea equestris* growing in crowded condition. Note the deeply cupped and crenulated lower (left) valve

clusters or those attached to protruding objects are grossly misshapen. Their length may exceed the height and the hinge side is distorted. The H/L ratio of this type varies from 0.68 to 0.95. The edge of the lower valve turned upward and had pronounced crenulations not noticeable in the flat specimens (Fig. 2).

The latter type is similar to the specimens from Charleston Harbor, South Carolina, collected by us from buoys and found also in the material in the U.S. National Museum obtained from the bottom of the same area.

Crowding not only influenced the size and shape of the shell, but affected the size and shape of the hinge and ligament as well. On flat and rounded oysters the hinge-line was symmetrical, the umbos and ligaments small and inconspicuous. On crowded and misshapen ones the hinge and ligaments were large and curved (Fig. 3). Gradual

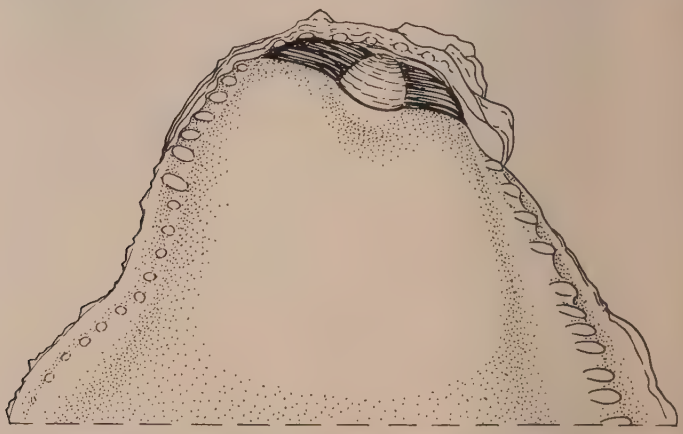


FIGURE 3. Ligament and denticles of *Ostrea equestris* 51 mm in height and 39 mm long. Upper part of the shell.

transition from one type to the other was evident when the oysters were arranged in one uninterrupted series.

The collection contains a number of specimens which grew over protruding objects such as bolts, barnacles, or small oysters. The plasticity of the shell-forming organ of *O. equestris* is so great that the underlying objects are faithfully duplicated and are even apparent on the upper valve which was not in direct contact with them.

The presence of a series of denticles along the lateral margins of

e upper valve is a prominent and persistent character which dis-nguishes young *O. equestris* from young *C. virginica*. The teeth may e rounded or oval-shaped and rib-like; often both of these conditions ist in the same specimen. The number and spacing of the denticles variable. In general, the larger the oyster the greater is the number of nticles. In some of the specimens, denticles extend along the anterior argin two-thirds of its length, in others they disappear at a distance less than one-third the length. The spacing, usually more uniform ear the umbo, becomes less regular away from the hinge and may be terrupted if the valves are misshapen (Fig. 4). In oysters measuring

GURE 4. Ligament and denticles of distorted shell *of O. equestris*. Upper part of the shell.

om 25 to 76 mm in height, the number of denticles along the anterior argin varied from 12 to 52. The first denticle is usually formed in rly postlarval specimens of 2 to 5 mm in height.

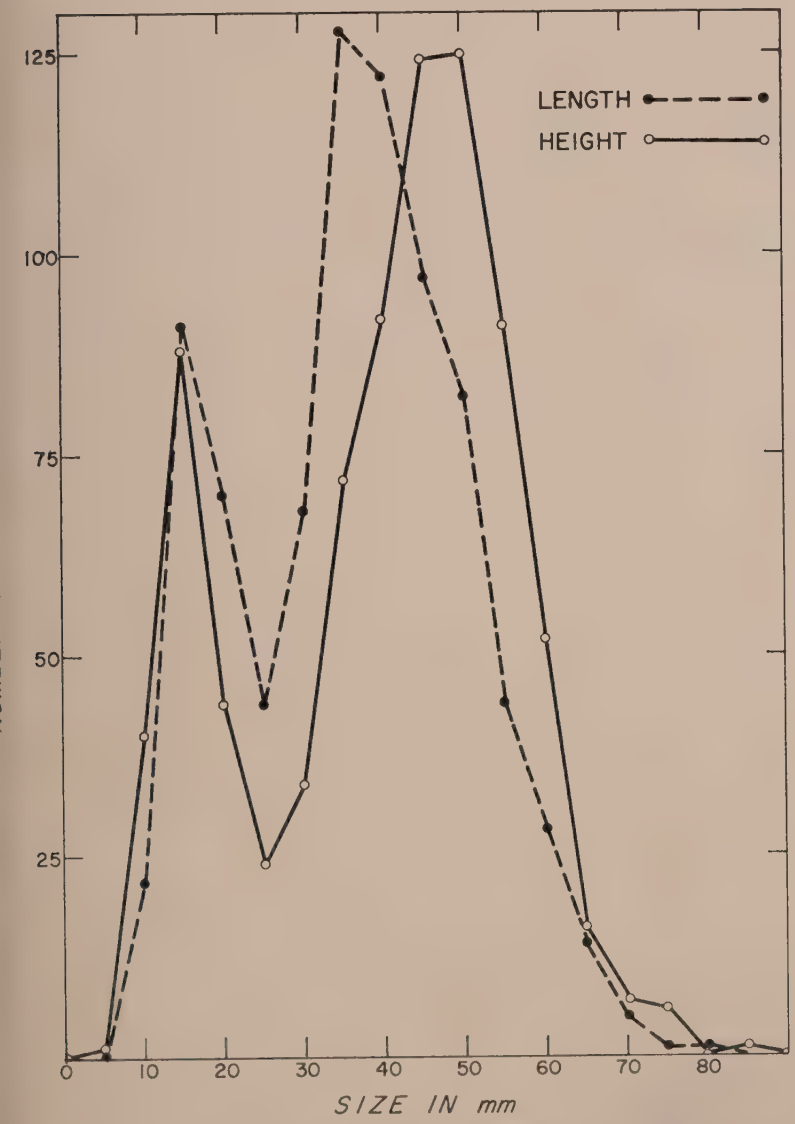
The variations in shell morphology described above reflect the fects of crowding and substrate on the population of oysters growing side the tube. This population probably developed from a brood of

larvae which originally found their way into the tube and settled on its wall. Since *O. equestris* is larviparous and the free-swimming period of larval life is short, it is reasonable to assume that the second generation of oysters are the descendants of the same brood. The observed variations cannot be associated with differences in latitude, climate, and salinity of water. They clearly reflect the effects of crowding and environment on shell morphology.

Oysters found on other buoys gave us new information on distribution at over 20 locations along the Atlantic Coast between Jacksonville, Florida, and Cape Lookout, North Carolina. These buoys, moored from ½ to 20 miles offshore, were in waters the surface salinities of which ranged from 33 to 36+‰ (according to the THEODORE N. GILL Cruise Reports 1-9, (Anderson, William W., et al., 1956-1959). In addition, we can report another interesting record. During DELAWARE cruise 60-7 on May 15, 1960, 10 specimens of *O. equestris* were dredged in an offshore area about half way between Delaware and Chesapeake Bays (37°31′N, 37°18′W) in 60 fathoms, bottom temperature 48.5°F. They were clumped to a rock on a bottom predominently mud-sand-shell. To our knowledge this is the most northern record for this species. These particular specimens have been separated into two lots, one of which has been sent to the U.S. National Museum, the other to the Museum of Comparative Zoology, Harvard University, for future reference.

The population gathered from the inner surface of the St. Mary's buoy stabilizer tube comprised two year classes as may be clearly seen in the bimodal frequency distribution of height and length (Fig. 5). One may deduce from these data that the median height for 1-year-old *O. equestris* is about 15 mm, and for 2-year-olds 45-50 mm. Because the buoy had been on station for almost 4 years other information regarding general rates of growth for buoy oysters was needed to confirm the possibility that the two modal groups actually represent two successive year classes. By sampling other buoys this additional evidence was obtained.

Because the buoys remain at their respective locations for known lengths of time it is possible to make a comparison of shell measurements on a time basis. For instance, the modal heights of *O. equestris* growing on 6 buoys which were out for about one year averaged from 17 to 29 mm. The modes of the oysters on 2 buoys exposed for one full year (November to November) averaged 18 and 20 mm respectively. Another buoy, stationed 5 miles off Bogue Bank, southwest of



IGURE 5. Frequency distribution of the height and length of shells of *Ostrea equestris* collected from a navigation buoy.

Beaufort Inlet, was out for 14½ months. This period included, however, the parts of the two growing seasons from June 4, 1943, to August 21, 1944. The sample taken from Bogue buoy comprised oysters with two modes at about 20 mm and 40 mm and some specimens as large as 57 mm. This represents a good rate of growth, particularly considering that the 130 oysters in this sample lot taken from a 2-foot square area on the buoy lived in crowded condition. The rate of growth of the oysters from the Bogue buoy compares favorably with that determined by Gunter (1951) for *O. equestris* from the template of an oil well platform in the Gulf of Mexico. The platform had been out one year from July 20, 1948, to July 17, 1949. His largest oyster measured 55 mm; the average size was 44.1 mm. Another time, 33 *O. equestris* were taken by Gunter from a Louisiana platform which had been pulled out on February 12, 1950, after remaining in the water 10 months and 10 days. These oysters ranged in size from 35 to 72 mm. Taking all the above evidence into consideration, we suggest that it is quite probable that the population of *O. equestris* on the St. Mary's buoy comprised distinct 1-and 2-year-old classes.

The rates of growth so far discussed for *O. equestris* refer to oysters suspended in the upper levels of the sea where growth generally is considered to be faster (Merrill, 1959). The largest specimen taken from the St. Mary's buoy measured 82 mm in height, quite possibly a record size for this species. *O. equestris* attached to buoy blocks on the bottom along the southeast Atlantic Coast are usually stunted and have thicker shells than those on a buoy above them. They rarely measure over 50 mm.

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AGE AND LENGTH COMPOSITION OF THE SARDINE CATCH OFF THE PACIFIC COAST OF THE UNITED STATES AND MEXICO IN 1959-60[1]

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INTRODUCTION

This report, the 14th on age and length composition of the catch of Pacific sardines *(Sardinops caerulea)* off the Pacific Coast of North America, resulted from one phase of the research conducted by the California Cooperative Oceanic Fisheries Investigations. Two CalCOFI agencies, the California Department of Fish and Game and the U.S. Bureau of Commercial Fisheries, have prepared these reports jointly on a seasonal basis since the 1941-42 sardine season (Wolf, *et al.*, 1961).

The assistance of Anita E. Daugherty and Clark Blunt, of the California Department of Fish and Game; and John MacGregor and Makoto Kimura of the U.S. Bureau of Commercial Fisheries, is gratefully acknowledged.

THE FISHERY

During the 1959-60 season, the 128-boat California sardine fleet landed 15,418 tons in central California and 20,335 in southern California for a total of 35,753. Approximately 8,113 of the 22,400 tons landed by the Mexican fleet were netted during a period comparable to the California season making a coastwide season total of 43,866 tons. This was less than half of the 110,414 tons landed the preceding season.

The catch was restricted little by cannery-imposed limits on individual boat trips. Limits, when imposed, ranged from 40 to 100 tons per boat per trip.

Central California

As in the previous year, the legal canning season in central California extended from August 1 through December 31. The seasons are set by California law, with Point Arguello as the central-southern area dividing line (Figure 2).

A price dispute deterred the fleet from fishing through all of August. On September 1, agreement was reached with five of the seven Monterey area canners, setting the price at $35 per ton for sardines and at $50 for mixed loads of sardines and mackerel.

Fishing began the night of September 1, and 1,571 tons were landed during the "September" dark-of-the-moon period. Lunar months are

[1] Submitted for publication May 1962.

FIGURE 1. A typical California sardine purse seiner that has just completed a haul. *(Photograph by Anita E. Daugherty, October, 1958.)*

set in quotation marks to distinguish them from the calendar months they approximate (Table 1). Almost equal tonnages were landed in "October," "November" and "December"—4,500, 4,000 and 4,400—and 800 in "January" giving a total through December 31 of 15,418, about 9,000 tons less than the preceding season.

The lower catch was caused in part by the late fishing start, and by inclement weather throughout much of September and October.

Ninety-four percent of the central California catch originated in or near Monterey Bay; the remainder was caught in the Morro Bay-Avila area and trucked to Monterey area processing plants. During the previous season, about two-thirds of the catch was netted off Morro Bay and Avila. In 1959, as in 1958, the fishermen paid the cost of shipping sardines from the Morro Bay area to the processing plants.

Seven canners processed the central California catch: five in Monterey, one in Moss Landing, and one in San Francisco. The fleet consisted of 13 large purse seiners (60 feet or over), 5 small purse seiners, and 20 lampara boats.

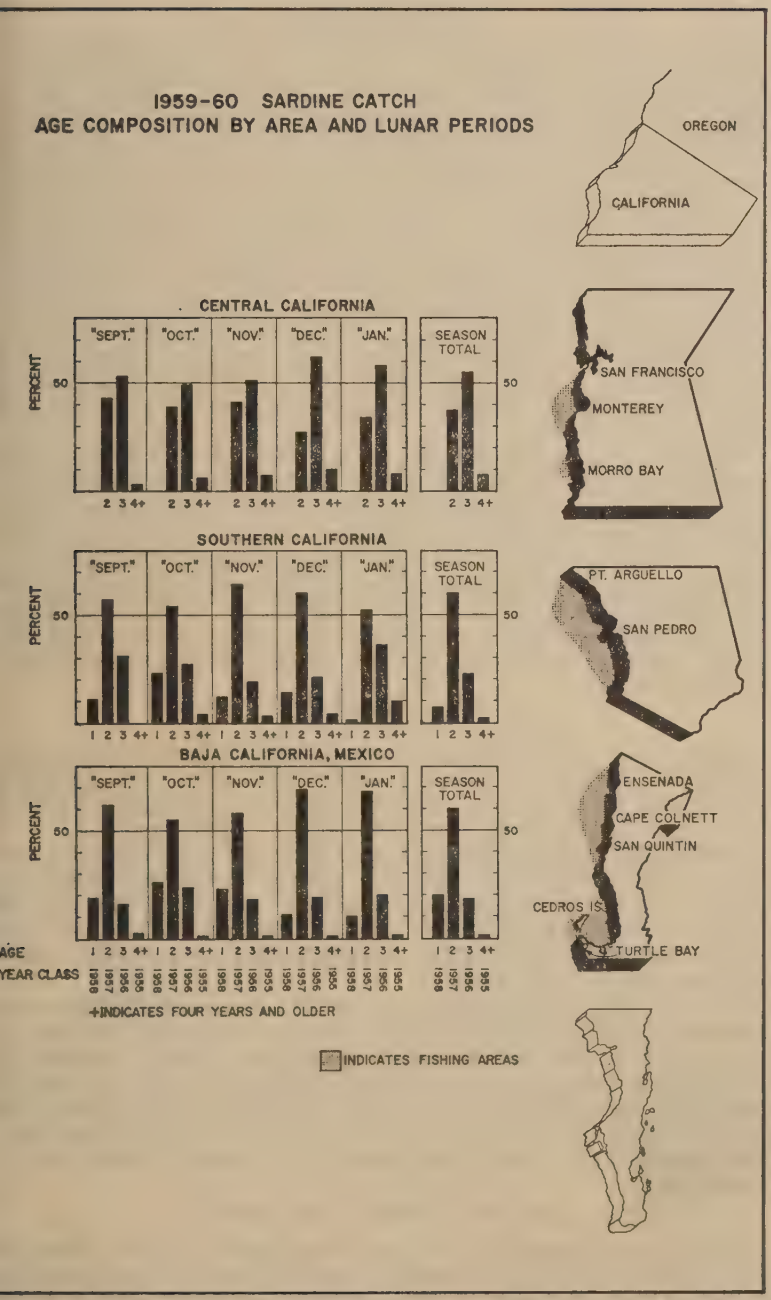

FIGURE 2. The sardine catch age composition by geographical area and lunar month periods. **Major fishing areas are shaded.**

Southern California

The southern sardine region extends from Point Arguello to the U.S.-Mexican border. The legal season began one month later than off the central coast, extending from September 1 through December 31. Although a few boats fished during September, the entire fleet did not fish until the night of October 4 due to price negotiations. At that time, the price was set at $35 per ton, the same as in central California.

For the second consecutive season, sardines were netted in the northwest portion of the region, with a few taken from the coastal area between San Pedro south to San Diego. Forty percent of the catches, as determined by fishermen interviews, originated in the expanse from the City of Santa Barbara to Point Mugu and offshore in the Santa Cruz Island-Anacapa Island area; 34 percent from Point Dume to Point Vicente and in Santa Monica Bay; 22 percent from southern Channel Island waters (Santa Barbara, Santa Catalina, San Clemente, and San Nicolas Islands); and 4 percent from the coastal area south of San Pedro.

Only 844 tons were landed during the "September" dark. Approximately 6,000 were netted in "October" which together with the 9,828 in "November" comprised 78 percent of the southern California total. About 2,500 tons were netted in "December" and 1,200 in "January" for a total southern California catch of approximately 20,335 tons.

Nine canners processed the southern California catch: eight in the Los Angeles-Long Beach Harbor area and one at Oxnard. Ninety boats supplied these processors, a decrease of 29 vessels from the previous season. The fleet consisted of 63 purse seiners (56 large, 7 small) and 27 lampara boats.

Baja California

There is year-round fishing for sardines off the Pacific coast of Baja California. During 1959, approximately 22,400 tons were netted by 20 Mexican purse seiners, 8,113 during the "September" through "January" darks. The catch was processed by eight canneries.

Mexican fishermen, operating cannery-owned boats, received a price equivalent to $15.10 (U.S. currency) per metric ton for sardines and mackerel. A few American seine fishermen from San Pedro and San Diego who delivered to Mexican canneries were paid $32.80 per metric ton for their fish. Sardines and mackerels used for reduction yielded fishermen $10.04 per metric ton.

The Baja California catch was netted in three general fishing areas: Ensenada, San Quintín, and Cedros Island (Figure 2). The six canneries at Ensenada were supplied by 14 boats fishing between Los Coronados Islands and Cape Colnett. A cannery at San Quintín operated two company-owned seiners in and around San Quintín Bay and the Cedros Island cannery took fish from four vessels which netted their catches in the area from northern Sebastián Vizcaíno Bay to Turtle Bay.

AGE AND LENGTH COMPOSITION

Lunar month summaries were used to obtain the year-class composition of the total catch following a method described by Felin and Phillips (1948). Inherent in the method are weight-per-fish factors computed each lunar week for each area. The average weights for this

ason were: central California 0.2449 pound, southern California 2041 pound, and Baja California 0.1487 pound.

The 708 fish aged from the central California catch were 2 through years old and ranged from 194 to 256 mm standard length (Table 2). n southern California, the 657 fish aged were 1 through 6 with lengths f 166 to 238 mm (Table 3). Ages ranged from 1 through 5 for 470 fish rom Baja California samples taken during the California season; their ngths ranged from 136 to 236 mm (Table 4). During the Baja Cali- rnia interseason, the 866 fish aged were 1 through 8 years old and 42 through 222 mm long (Table 5).

Two- and three-year-old fish constituted 92 percent of the 115,943,000 ardines caught in central California (Figure 2 and Table 6). The ree-year-old 1956 year-class contributed 54 percent and the two-year- ld 1957 year-class, 38 percent. There was little change in length or ge composition between lunar periods.

In southern California, the 1957 year-class as two-year-olds con- ibuted 60 percent of the 202,095,000 sardines caught, the three-year- ld 1956 year-class 23 percent, and the one-year-old 1958's 12 percent Figure 2 and Table 6).

In Baja California, during the California season, the 1957 year-class pplied 61 percent of the 118,672,000 fish netted (Table 6). One-year- lds, of the 1958 year-class, contributed 20 percent and three-year-olds, ne 1956 year-class, 18 percent.

During the interseason, from January 1 to September 1, the Baja alifornia catch of 189,008,000 sardines contained 47 percent three- ear-olds, 1956 year-class (Table 7). The two-year-old 1957 year-class ontributed 39 percent and the four-year-old 1955's, 8 percent.

TABLE 1
Calendar Dates of Lunar Months During 1959

Lunar month	Lunar period[1]	Dates
"January"	485	December 25–January 23
"February"	486	January 24–February 21
"March"	487	February 22–March 23
"April"	488	March 24–April 22
"May"	489	April 23–May 22
"June"	490	May 23–June 20
"July"	491	June 21–July 20
"August"	492	July 21–August 18
"September"	493	August 19–September 17
"October"	494	September 18–October 16
"November"	495	October 17–November 15
"December"	496	November 16–December 14
"January"	497	December 15–January 12[2]

[1] Lunar periods have been numbered serially since "November" of the 1919-20 season.
[2] All commercial sardine fishing was considered to end on December 31.

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TABLE 2

Length Composition of Year-Classes in Sardine Samples from the Central California Commercial Catch, 1959-60 Season

Age	2	3	4	5	6	
Year-class	1957	1956	1955	1954	1953	Total
Standard length mm						
194	--	1	--	--	--	1
196	5	2	--	--	--	7
198	7	5	--	--	--	12
200	10	9	1	--	--	20
202	11	17	0	--	--	28
204	27	22	2	--	--	51
206	32	24	3	--	--	59
208	40	44	3	--	--	87
210	37	51	7	1	--	96
212	34	48	10	1	--	93
214	27	33	7	--	--	67
216	15	36	1	--	--	52
218	16	29	3	--	--	48
220	7	27	2	--	--	36
222	7	8	2	--	--	17
224	2	8	2	--	--	12
226	4	5	0	--	--	9
228	--	5	0	--	--	5
230	--	1	0	--	--	1
232	--	1	1	--	--	2
234	--	0	2	--	--	2
236	--	0	1	--	--	1
238	--	0	0	--	--	0
240	--	0	0	--	--	0
242	--	0	0	--	--	0
244	--	0	0	--	--	0
246	--	0	1	--	--	1
248	--	0	--	--	--	0
250	--	0	--	--	--	0
252	--	0	--	--	--	0
254	--	0	--	--	--	0
256	--	1	--	--	--	1
Totals	281	377	48	2	--	708
Mean lengths	210	212	215	211	--	211

TABLE 3

Length Composition of Year-Classes in Sardine Samples from the Southern California Commercial Catch, 1959-60 Season

Age	1	2	3	4	5	6	
Year-class	1958	1957	1956	1955	1954	1953	Total
Standard length mm							
	1	--	--	--	--	--	1
	0	1	--	--	--	--	1
	0	2	1	--	--	--	3
	4	4	0	--	--	--	8
	0	2	0	--	--	--	2
	7	13	0	--	--	--	20
	8	6	1	--	--	--	15
	3	17	1	--	--	--	21
	15	24	2	--	--	--	41
	7	13	1	--	--	--	21
	4	18	1	--	--	--	23
	6	16	5	--	--	--	27
	3	20	3	1	--	--	27
	4	25	7	1	--	--	37
	1	19	9	2	--	--	31
	0	20	4	3	--	--	27
	2	21	12	1	--	--	36
	0	16	12	3	--	--	31
	1	19	8	1	--	--	29
	0	30	14	2	--	--	46
	0	25	23	2	--	--	50
	1	27	17	0	--	--	45
	--	9	13	1	--	--	23
	--	17	12	2	--	--	31
	--	13	8	4	--	--	25
	--	8	5	2	--	--	15
	--	1	2	0	--	--	3
	--	2	2	0	1	--	5
	--	1	0	1	0	1	3
	--	--	3	0	0	--	3
	--	--	1	0	0	--	1
	--	--	0	0	0	--	0
	--	--	0	1	0	--	1
	--	--	1	0	1	--	2
	--	--	0	0	0	--	0
	--	--	0	1	0	--	1
	--	--	1	--	1	--	2
Totals	67	389	169	28	3	1	657
Mean lengths	183	196	204	207	230	222	197

TABLE 4

Length Composition of Year-Classes in Sardine Samples from the Baja California Commercial Catch, 1959-60 ("September" through "December")

Age	1	2	3	4	5	
Year-class	1958	1957	1956	1955	1954	Total
Standard length mm						
136	1	--	--	--	--	1
138	1	--	--	--	--	1
140	0	--	--	--	--	0
142	1	--	--	--	--	1
144	3	1	--	--	--	4
146	0	0	--	--	--	0
148	4	2	--	--	--	6
150	2	3	--	--	--	5
152	6	2	--	--	--	8
154	10	6	--	--	--	16
156	7	7	--	--	--	14
158	15	12	2	--	--	29
160	11	16	3	--	--	30
162	7	18	3	--	--	28
164	7	26	1	--	--	34
166	8	22	3	--	--	33
168	2	16	1	--	--	19
170	0	31	8	--	--	39
172	2	17	4	--	--	23
174	0	16	5	--	--	21
176	0	18	10	--	--	28
178	0	12	13	1	--	26
180	1	12	7	2	--	22
182	--	11	7	0	--	18
184	--	6	8	0	--	14
186	--	6	8	2	--	16
188	--	2	5	0	--	7
190	--	4	5	0	--	9
192	--	2	2	0	--	4
194	--	1	1	0	--	2
196	--	2	0	0	--	2
198	--	1	1	1	--	3
200	--	1	1	0	--	2
202	--	--	0	1	--	1
204	--	--	0	0	--	0
206	--	--	0	1	--	1
208	--	--	0	--	--	0
210	--	--	2	--	--	2
236	--	--	--	--	1	1
Totals	88	273	100	8	1	470
Mean lengths	158	170	179	190	236	170

TABLE 5

Length Composition of Year-Classes in Sardine Samples from the 1959 Baja California Interseason Catch ("January"-"August")

Year-class	1958	1957	1956	1955	1954	1953	1952	1951	Total
Standard length mm									
2	1	--	--	--	--	--	--	--	1
4	0	--	--	--	--	--	--	--	0
6	1	3	--	--	--	--	--	--	4
8	1	1	--	--	--	--	--	--	2
0	3	1	--	--	--	--	--	--	4
2	3	6	1	--	--	--	--	--	10
4	2	3	1	--	--	--	--	--	6
6	6	11	1	--	--	--	--	--	18
8	0	13	5	1	--	--	--	--	19
0	1	20	10	0	--	--	--	--	31
2	0	12	8	1	--	--	--	--	21
4	3	22	9	0	--	--	--	--	34
6	0	14	9	0	--	--	--	--	23
8	1	19	13	1	--	--	--	--	34
0	0	12	11	1	--	--	--	--	24
2	1	18	8	1	--	--	--	--	28
4	0	12	15	1	--	--	--	--	28
6	0	21	12	1	--	--	--	--	34
8	0	16	16	1	--	--	--	--	33
0	1	11	19	2	--	--	--	--	33
2	--	10	12	1	--	--	--	--	23
4	--	19	35	0	--	--	--	--	54
6	--	9	32	7	--	--	--	--	48
8	--	20	35	5	--	--	--	--	60
0	--	19	37	7	--	--	--	--	63
2	--	8	38	4	--	--	--	1	51
4	--	8	38	5	--	--	--	--	51
6	--	4	20	9	--	1	--	--	34
8	--	4	15	5	--	--	--	--	24
0	--	1	12	6	--	--	--	--	19
2	--	2	6	4	--	--	--	--	12
4	--	2	4	5	--	--	--	--	11
6	--	--	3	5	2	--	--	--	10
8	--	--	1	2	1	--	--	--	4
0	--	--	3	4	0	--	--	--	7
2	--	--	0	0	0	--	1	--	1
4	--	--	0	0	0	--	--	--	0
6	--	--	0	4	1	--	--	--	5
8	--	--	0	0	--	--	--	--	0
0	--	--	1	0	--	--	--	--	1
2	--	--	--	1	--	--	--	--	1
tals	24	321	430	84	4	1	1	1	866
ean lengths	157	174	185	195	209	196	212	192	181

TABLE 6

Age and Year-Class Composition of the Sardine Catch in the 1959-60 Season

	Catch		Number of fish in thousands by age and year-class						
			1	2	3	4	5	6	7
	Tons	Number	1958	1957	1956	1955	1954	1953	1952
Central California									
"August"	--	--	--	--	--	--	--	--	--
"September"	1,571	11,274	--	4,882	5,998	304	90	--	--
"October"	4,544	34,049	--	15,186	16,684	2,179	--	--	--
"November"	4,068	31,439	--	12,953	16,129	2,106	220	31	--
"December"	4,435	33,083	--	9,065	20,511	3,408	99	--	--
"January"[2]	800	6,098	--	2,122	3,537	341	98	--	--
Total Central California	15,418	115,943	--	44,208	62,859	8,338	507	31	--
Percent	--	100.0	--	38.1	54.2	7.2	0.5	--	--
Southern California									
"September"	844	6,853	774	3,934	2,145	--	--	--	--
"October"	5,942	60,039	8,045	32,661	16,571	2,642	60	60	--
"November"	9,828	100,581	12,372	65,177	19,412	2,917	603	100	--
"December"	2,531	24,473	3,573	14,684	5,188	979	49	--	--
"January"	1,190	10,149	142	5,277	3,715	873	112	--	30
Total Southern California	20,335	202,095	24,906	121,733	47,031	7,411	824	160	30
Percent	--	100.0	12.3	60.2	23.3	3.7	0.4	0.1	--
Total California	35,753	318,038	24,906	165,941	109,890	15,749	1,331	191	30
Percent	--	100.0	7.8	52.2	34.6	4.9	0.4	0.1	--
Baja California[3]									
"September"	1,326	20,051	3,887	12,413	3,220	531	--	--	--
"October"	2,405	35,874	9,354	19,893	6,360	267	--	--	--
"November"	2,017	31,054	7,134	18,059	5,694	167	--	--	--
"December"	1,545	20,721	2,215	14,289	3,951	85	181	--	--
"January"[2]	820	10,972	1,132	7,462	2,224	52	102	--	--
Total Baja California	8,113	118,672	23,722	72,116	21,449	1,102	283	--	--
Percent	--	100.0	20.0	60.8	18.1	0.9	0.2	--	--
TOTAL	43,866	436,710	48,628	238,057	131,339	16,851	1,614	191	30
Percent	--	100.0	11.1	54.5	30.1	3.9	0.4	--	--

[1] Price dispute, vessels did not fish.
[2] December 15 to January 1 only.
[3] Includes data from Ensenada, San Quintín and Cedros Island.

TABLE 7

Year-Class Composition of the 1959 Interseason Sardine Catch for Baja California

Lunar month	Catch		Number of fish in thousands by age and year-class							
			1	2	3	4	5	6	7	8
	Tons	Number	1958	1957	1956	1955	1954	1953	1952	1951
uary"[1]	1,298	19,804	--	9,169	10,535	80	20	--	--	--
ruary"	1,147	16,350	--	3,705	10,240	2,405	--	--	--	--
rch"	1,255	17,591	--	4,363	10,550	2,273	289	--	116	--
ril"	1,317	19,407	--	9,845	7,621	1,494	--	447	--	--
y"	821	12,315	1,296	5,187	5,184	648	--	--	--	--
e"	4,634	60,207	6,337	25,351	25,349	3,170	--	--	--	--
y"	1,792	20,680	419	5,869	11,597	2,795	--	--	--	--
gust"	1,646	18,100	786	8,812	6,900	1,155	--	--	--	447
tember"[2]	415	4,554	415	2,168	1,653	318	--	--	--	--
AL	14,325	189,008	9,253	74,469	89,629	14,338	309	447	116	447
ent	--	100.0	4.9	39.4	47.4	7.6	0.2	0.2	0.1	0.2

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No. 3.
The Gulf III and other Modern High-Speed Plankton Samplers

By

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velopment of Gulf III Plankton Sampler

A high-speed plankton sampler was developed in 51 for use in an inventory of the biological condi-ns in the Gulf of Mexico being conducted by the ited States Fish and Wildlife Service's Gulf Fishery vestigations. It was believed that a more adequate imation of the relative abundance of zooplankton, rticularly fish larvae and other agile organisms, uld be obtained by towing a large-mouth sampler higher speeds than possible with the standard silk tre and half-metre nets. Also, the need to estimate e volume of water filtered after it had passed through e net prompted investigation of the feasibility of closing a half-metre net of metal cloth in a protec-e metal cylinder, and mounting a flow meter in e after end.

Four requirements were established for the desired mpler:—

- construction of corrosion resistent metal capable of withstanding towing speeds in excess of 5 knots (2·6 m/sec.);
- as large a mouth opening as was feasible for towing at 5 knots and still allow for effective filtration of the water entering the sampler;
- attachment of towing cable behind sampler open-ing to eliminate disturbance ahead of sampler mouth;
- in addition to the flow meter in the mouth of the sampler, placement of a flow meter behind the net, so that flow through the net might be estimated.

We were aware of no design incorporating all four these features. The plankton sampler designed ich incorporated them was designated as model Gulf III", and was the third in a series of samplers signed for specific uses by the Gulf Fishery Invest-igations (Gehringer, 1952). The Gulf III was con-structed entirely of monel metal. The filtering mechan-ism was a conical, metal cloth net 19·5 inches (49·5 cm) in diameter and 54 inches (137 cm) in length, fitted at its cod-end with a detachable metal cup, and a flow meter suspended in the fore end. This net was enclosed in a metal cylinder 19·75 inches (50·2 cm) in diameter and 60 inches (152 cm) in length. A removeable nose-piece reduced the opening to 16 inches (40·7 cm), and a removeable tail section 16 inches (40·7 cm) in diameter and 24 inches (60·9 cm) in length housed a flow meter. Three stabilizing fins were attached at the rear of the net housing. The towing and depressor cables were attached at the top and bottom respectively, to a pipe ring fitted around the front of the net housing. The filtering unit was of monel metal cloth, 50 mesh to the inch, of 0·0075 inch wire (selected to approximate No. 1 silk bolting cloth), supported by a rigid framework of rings and rods. With these wire and mesh measure-ments the ratio of area of nose-piece opening to open area of the filtering screen was 1:3·6, which was believed adequate for the density of plankton expected. A depressor weighing 40 pounds (18·2 kg) designed by John Isaacs, Scripps Institution of Oceanography (Marine Research Committee, 1950) was used to hold the sampler at the desired depth. Launching and retrieving were accomplished with the vessel underway at towing speed, approximately 5 knots (2·6 m/sec.).

Trial tests for stability during towing, durability at speeds in excess of 5 knots, and condition of plankton organisms taken at these speeds were encouraging. Because of interest shown by other workers, it was decided to publish a description of the sampler even though testing had not been completed. The original design was described and figured along with the design

ontribution No. 66
S. Fish & Wildlife Service
ureau of Commercial Fisheries
iological Laboratory

of a high-speed sampler having a small aperture, the Gulf I-A (Arnold, 1952).

Collections with the Gulf III at 4 to 5 knots (2·1–2·6 m/sec.) as compared with those of a standard half-metre silk net at 1 knot (0·5 m/sec.) during an M. V. "Alaska" cruise in the Gulf of Mexico in January 1952, showed that the Gulf III was equally as effective in the capture of smaller organisms and more efficient in capture of the larger organisms, and it was used on subsequent cruises (Arnold, 1958). A partial analysis of the results of the plankton investigations (Arnold, 1958) supports the contention that the Gulf III is an improvement over the half-metre silk net.

We used a modified version of the Gulf III on M. V. "Theodore N. Gill" cruises 3 through 9 during 1953 and 1954 in a survey of plankton organisms in the waters off the south Atlantic coast of the United States. These modifications were described by Anderson and Gehringer (1957), and consisted of: attachment of towing cable to the sampler with a two-leg chain bridle; introduction of a shock absorber (commercial vibro-hanger used in aircraft construction) between towing cable and sampler bridle to reduce effect of vibration of towing cable and help absorb stresses during surges; fitting the cod-end of the filtering unit with a ring stand to permit standing the unit while the plankton was washed into the terminal bucket; and the use of wire cloth having wire of 0·008 inches diameter,rather than 0·0075 inches as in the original version (this was not by choice, but because mesh with wire of 0·0075 inches diameter was not available).

Later the depressor as well as the towing cable was secured to the sampler by a two-leg chain bridle. Both towing and depressor lines were attached to the same rings on the sides; an arrangement which permitted the sampler to pivot freely in the vertical plane. With the original method of attaching the cables, the depressor could exert sufficient force to flip the tail of the sampler if the depressor caught a wave during launching or retrieving.

The meter in the tail section was used to estimate the flow through the sampler as irregular, unexplained inconsistencies occurred in fore meter readings. Periodic calibration of the flow meters by towing the sampler housing, *sans* filtering screen, over a calculated course between two marker buoys several miles off the coast at normal towing speed of 4–6 knots (2·1–3·1 m/sec.) provided basic figures upon which water volumes were estimated. Replacement of the original glass jewels in the Atlas type current meter with miniature ball bearings improved performance of the meter.

A modification of the Gulf III sampler was constructed for the U. S. Bureau of Commercial Fisheries Biological Laboratory, Juneau, Alaska, primarily for sampling of herring larvae. Unfortunately the sampl was lost with the sinking of the vessel "Mackinaw" 1960, and was not replaced. Their work with t sampler concerned primarily the calibration of t instrument, and little actual sampling of herring larv was conducted. The modifications were basically th described by Bridger (1958); hinging the tail secti and reducing the nose cone to an 8-inch (20·3 cm) d meter. George Y. Harry, Laboratory Director, pr vided the following information (personal commu cation).

Analysis was made of the catch rate for the samp for comparable tows (speed of 7 knots (3·6 m/sec horizontal, at 100 m depth), day and night, with and 8-inch (40·7 cm and 20·3 cm) nose-pieces. T analysis of variance revealed significant differences numbers of *Sagitta* sp. captured by the net betwe day hauls and night hauls, between sizes of nose con and in the catch of nose cones of different size at nig and in the day. Tows during daylight hours with t 8-inch (20·3 cm) nose cone indicated higher numb of *Sagitta* sp. per m^3 of water than were indicat with the 16-inch (40·7 cm) nose cone. Night-tim catches per m^3 of water with the 8-inch (20·3 cm) no cone were considerably higher than with the 16-in (40·7 cm) cone. Change in direction of towing ga no significant difference in numbers of *Sagitta* capture

John B. Colton, Jr., U. S. Bureau of Commerc Fisheries Biological Laboratory, Boothbay Harbo Maine, reported (personal communication) "We ha used this gear a few times in connection with larv fish surveys in restricted areas. In these situations t sampler worked satisfactorily, although our particul model was rather fragile". Objections to the samp for their use were: impracticability to tow sampler series, and absence of a closing device.

Other Modern High-Speed Plankton Samplers

Catcher. Of the numerous high-speed samplers whi have been described recently, only the Catcher, d scribed by Bary *et al.* (1958), has the size mouth ope ing (9 inches or 22·9 cm) comparable to that of t Gulf III and also meters the flow out of the sampl

Gulf V. The U. S. Bureau of Commercial Fisher Biological Laboratory, Galveston, Texas, has be using the Gulf V plankton sampler (Arnold, 1959) a shrimp fishery investigation since 1956. Basicall the Gulf V is a conical, monel metal mesh net inches (40·7 cm) in diameter at the mouth and inches (137 cm) in length.

Gulf I-A. Arnold, U. S. Fish and Wildlife Servic Gulf Fishery Investigations, Galveston, Texas, d

cbed (1952) a high-speed plankton sampler, de- ıated as Gulf I-A, designed for towing at the end ıı cable, at or near the surface, at a speed of 9 to knots (4·6 to 5·2 m/sec.).

Gulf-II. A semi-automatic plankton sampler, de- ıated the Gulf-II, was developed in 1951 by the S. Fish and Wildlife Service's Gulf Fishery Investi- ions for study of the patchiness of plankton distri- ıtion near the surface (Collier, 1957). This was a stitute for the Continuous Plankton Recorder ardy, 1936), which at that time was not available the laboratory.

saacs Sampler. A high-speed plankton sampler was eloped by personnel of the U. S. Fish and Wildlife vice's South Pacific Fishery Investigations and ipps Institution of Oceanography, La Jolla, Cali- nia, for obtaining "information on plankton distri- tion by taking a strip sample while the ship was ning full speed ahead between stations" (Ahlstrom *al.*, 1958). It has an overall length of 51 inches 30 cm), a diameter of 3 inches (7·6 cm) with a mouth ening of 1 inch diameter (2·5 cm).

Small Plankton Samplers. The Plankton Indicator, a gh-speed sampler with small aperture, was designed A. C. Hardy, University College, Hull, England, the early 1920's for use by commercial herring ermen to determine any possible relationship be- een amount and type of plankton and the number herring in the immediate vicinity (Hardy, 1926). is a basic unit which has since been modified by ardy and others (see Henderson, Lucas and Fraser 936) for details of construction).

The Small Plankton Sampler was designed by S. Glover (1953), Oceanographic Laboratory, Scot- h Marine Biological Association, Edinburgh, for ultaneous sampling at four or five different depths m 10 m to 50 m. Whereas the Indicators designed Hardy collected the sample on a disc of silk secured a metal ring in the after end of the sampler, Glover's mpler used a nylon net $3^1/_2$ inches (8·9 cm) long ld in position by the nose-piece.

Multi-depth Plankton Indicator. More recently Glover 961) described the Multi-depth Plankton Indicator, ed since 1955 by the Edinburgh Oceanographic aboratory's plankton programmes to sample simul- neously at five different depths. It includes new ethods of securing the silk disc and net, and casting e towing eye and nose in one piece. The fixed towing e consists of a cup with a sloping slot situated to rmit the eye to slip over the cable when the sampler twisted and swiveled in a specific path.

Miller Sampler. David Miller, U. S. Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Mass., described (1961) a modified small Hardy plankton sampler, based on the design described by Glover in 1953, designed to study the vertical distribution of the haddock larvae within areas where they were concentrated. The sampler is relatively inexpensive, costing approximately 75 dollars per unit. Tests on the filtering capacity of the sampler indicate relatively constant capacity with several mesh sizes at towing speeds of 5 to 10 knots (2·6 to 5·2 m/sec.). There are indications that daytime escapement of active zooplankton forms, generally encountered in the use of slow-moving nets, is virtually eliminated with this sampler (Miller, 1961).

Motoda's High-speed Samplers. Sigeru Motoda, Hokkaido University, Hakodate, Japan, has described several high-speed plankton samplers. Three of these are designed for towing singly, at the surface, at running speed, and to collect several separate portions during a single tow (Motoda, 1953, 1959, models 18 and 19).

Motoda has also described several Underway Plankton Catchers which are designed to take a single sample, and to be towed singly at running speed (Motoda, 1954, 1959, models 16 and 17).

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Discussion

(This paper was presented by Rear Admiral C. W. Thomas and was followed by a contribution by Dr. C. J. Fish included here as No. 3A).

In the discussion of the two papers Dr. Fish said that the Gulf III sampler can be towed up to 7 knots and the new titanium model up to 10 knots at depths down to 1,000 metres: at that depth he estimated that between 4,000 and 5,000 metres of wire would be needed with a 40 lb weight. Dr. Kinzer stressed the need for more effective depressors and suggested the use of kite otters. Dr. Cushing reported that a Gulf III sampler of twice the original size had been made at Lowestoft and smaller nets and a water bottle are being attached to it: a kite otter is used as a depressor. Mr. Vagn Hansen thought that this increase in size is necessary for catching fish larvae, and quoted comparative hauls in Danish waters where a 2 metre stramin net caught large quantities of whiting larvae and the Gulf III none at all.

During a discussion on the difference between night and day catches it was agreed that escape in daylight plays a part as well as vertical migration, and neither by itself can account for all the observations. It was also suggested that in some places small fish might not be caught at night because of phosphorescence on the net.

BIANCO LUNO A/S, KBH

STUDIES OF FISH LARVAE FROM ALONG THE SOUTH ATLANTIC COAST OF THE UNITED STATES

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A study is presently under way which is concerned with the identification, distribution, and abundance of fish larvae in the waters off the south Atlantic coast of the United States between Cape Hatteras, North Carolina, and the Straits of Florida from the shore out into the Gulf Stream. The knowledge of the identity of the larval forms is a prerequisite to the establishment of growth and development, spawning times and areas, geographical ranges, abundance, and dispersal of the species in the area. Some species are important as commercial or sport fishes, others are important as forage, and some have no apparent value other than an undetermined position in the fauna of the area.

The dependence upon both marine and estuarine habitats for successful development and reproduction has been demonstrated for a number of species. For example, shad and striped bass live primarily in marine environment but return to fresh water to spawn. One of the mullets lives in fresh water, but spawns in the ocean. The ten-pounder spawns at sea, and the young reach the estuarine waters as leptocephalid larvae and mature in inside waters. The striped and silver mullets, several species of the jack crevalles, the pompanos, and menhaden spawn at sea, but also use the estuarine habitat during a portion of their development. The most important commercially of marine forms requiring both estuarine and marine habitats are the white, pink, and brown shrimp, which hatch at sea, reach the marshes through influence of the tides, develop there, and then move out as juveniles.

We have knowledge of the early development of but a few of our ...ine fishes, and suspect our studies will reveal that development for a ...siderable number of the fishes is dependent upon both habitats. We can... overemphasize the importance of maintaining the estuarine habitat for ... successful development of many of our important species of marine ...nals. As pointed out by W. W. Anderson in a progress report to the ...antic States Marine Fisheries Commission meeting in Charleston, S.C., ...960, our studies make clear the link between the estuarine environment ... the offshore Continental Shelf area (and even the Gulf Stream) is much ...ser in relation to pertinent phases of the life history of many species than ... suspected.

Our basic study material was derived from plankton samples taken ...r the study area during nine cruises of the Theodore N. Gill during 1953 ...1954. Supplemental material is obtained from seine samples from ...ch and estuarine habitats.

Knowledge of the early life history of the majority of marine species ...meager at best, and consequently the reference literature is weak. For ... identifications we cannot make use of published figures and descriptions, ... reference to identified material in museums. We have two choices as to ... method of arriving at the identity of the larval forms. The first is to ...ch and rear the larvae from identified eggs, which means capture of ...lts in spawning condition and application of techniques for rearing in ...ually less than optimum conditions aboard ship. Whereas this system has ...t with success in some instances, death of the larvae upon absorption of ... yolk sac is the usual end, if hatching occurs at all. The second method, ... the one being used in this study, is to retrace development of anatomical ...aracters in identified juveniles or adults back down through successively ...aller material.

The several steps involved in our approach are as follows: separa... of fish larvae from the plankton samples, sorting to the various dis... forms in each sample, photographing each distinct form in each sample ...h a 35 mm. camera mounted on one eyepiece of a stereomicroscope ...rial numbers photographed with the specimen identify the specific larva, ...ch permits subsequent grouping of larvae of similar form by sorting ...tographic prints rather than requiring actual handling of the specimens), ...signment of specific families, genera, or forms to the various staff mem... for identification, if possible, and illustration and description by

species, or illustration and description as size series of undetermined species or forms. Several publications of which parts are the result of this project include studies on the Atlantic sailfish, swordfish, three species of mullet, ten-pounder, the jack crevalles, tarpon, the filefishes; and several in press include studies on one of the bigeyes, the rudderfishes, the pompanos, the goatfishes, and menhaden. At present we are well into sorting and photographing the types in each sample. Assembly of an Atlas of published illustrations of fish larvae and eggs is underway, which will prove of considerable value in these studies.

Although our principal concern at the present is with the larvae, study of the fish eggs will be initiated when studies on larvae of specific species indicate identity of a particular type of egg is possible.

Future efforts will be devoted to completing the studies presently under way, and subsequently, the study of this material as related to and influenced by chemical and physical properties of the water, which was sampled concurrently with the taking of biological data and material and subsequently analyzed for several constituents.

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Main Topic
I

Paper No.
R/I.1

THE WORLD BIOMASS OF MARINE FISHES

La biomasse mondiale des poissons marins

La biomasa mundial de los peces marinos

by

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, Italy

bstract

Many people believe that the 300 million cubic miles of salt water in the oceans have a omparably vast potential as a source of protein food. Under present conditions, however, there s a definite limit to this protein potential, at least insofar as marine fish are concerned.

The most productive fishing areas are various grounds on continental shelves, especially in he northern hemisphere and in areas of the oceans where phytoplankton production is relatively igh. Many of these areas are probably approaching peak production now. A computation of otential world harvest, based on the catch of fish per unit area on representative productive ontinental shelf areas, yields an estimated annual harvest potential of 55 million metric tons.

Using the estimated net primary production in all oceans as another basis for computation, t is estimated that approximately 115 million metric tons of marine fish are potentially vailable for harvest annually. However, a large portion of this production is too thinly cattered to be economically fished at this time.

It is shown that a relation exists between fish catch and benthic biomass. Inasmuch as he benthic biomass decreases very rapidly with depth, one cannot expect any substantial opulation of fishes on the bottom beyond the continental shelves.

There appears to be no reason to suggest that, under present conditions and with present ishing techniques, the annual harvest of marine fishes can be more than doubled or, at the very ost, tripled. It is estimated that a reasonable expectation might be about 60 million metric ons annually.

ésumé

Beaucoup de personnes croient que les 300 millions de milles cubiques d'eau salée des céans représentent un potentiel relativement vaste comme source d'aliments protéiques. Sous es conditions actuelles, cependant, il existe une limite définie à ce potentiel protéique, au oins en ce qui concerne les poissons marins.

Les zones de pêche les plus productives sont des fonds divers sur les plateaux continentaux, pécialement dans l'hémisphère nord et dans les régions océaniques où la production de phyto- lancton est relativement haute. Un calcul de la récolte potentielle mondiale, basée sur la uantité pêchée par unité de surface sur les zones de production représentatives du plateau ontinental, permet d'estimer à 55 millions de tonnes métriques le potentiel annuel de récolte.

En prenant comme autre base d'appréciation la production primaire nette estimée de tous es odéans, on arrive à chiffrer à 115 millions environ de tonnes la quantité de poisson isponible en puissance pour être récoltée chaque année. Cependant, une large part de cette roduction est trop clairsemée pour être pêchée d'une manière économique durant cette période.

Il est démontré qu'une relation existe entre la capture du poisson et la biomasse benthique. tant donné que la biomasse benthique décroît très rapidement avec la profondeur, on ne peut 'attendre à trouver une population substantielle de poissons sur le fond au delà des plateux ontinentaux.

Il semble ainsi qu'il n'y ait pas de raison de penser que, sous les conditions actuelles t avec les présentes techniques de pêche, la récolte annuelle de poissons marins puisse être lus que doublée, voire triplée. On peut estimer les possibilités raisonnables à 60 millions nviron de tonnes métriques par an.

Resumen

Cree mucha gente que los 300 millones de millas cúbicas de agua salada en los océanos tienen un vasto potencial comparable, como fuente de alimento proteico. Sin embargo, en las circunstancias actuales hay un límite claro a este potencial, por lo menos en cuanto se refiere a los peces marinos.

Las zonas pesqueras más productivas son varios bancos en las plataformas continentales, especialmente en el hemisferio norte, y en regiones oceánicas en las que la producción de fitoplancton es relativamente elevada. Muchas de estas regiones probablemente se aproximan a su producción máxima en estos momentos. El cómputo de la cosecha mundial potencial, basado en la pesca por unidad de volumen en puntos representativos productivos de la plataforma continental, da un potencial de pesca anual estimado en 55 millones de toneladas métricas.

Empleando la producción primaria neta estimada para todos los océanos como base del cómput se calcula que hay una disponibilidad potencial de 115 millones de toneladas métricas de peces para cosecharlos anualmente. Sin embargo, una gran proporción de esta cantidad no está lo suficientemente concentrada para pescarla económicamente en la actualidad.

Se sabe que existe una relación entre las capturas y la biomasa del bentos. Dado que la biomasa del bentos decrece muy rápidamente con la profundidad, no se puede esperar que existan poblaciones substanciales de peces en el fondo, más allá de las plataformas continentales.

No parece que existan razones para sugerir que en las condiciones y con las técnicas de pesca actuales la cosecha anual de peces marinos se pueda duplicar o, a lo sumo, triplicar. Se estima que una espectativa razonable podría ser alrededor de 60 millones de toneladas métric anuales.

Every cubic mile of sea water contains 140 pounds of gold. At this thought you might well ask, what kind of a sieve do I need to strain out this valuable metal? Granted you had the perfect sieve, it would not be practical to remove the gold. A little calculation will show that to strain one cubic mile of sea water through any kind of device would require pumping 50,000 gallons of water every second continuously for one year, obviously an impractica procedure.

We are continuously bombarded by press, radio, and scientific articles with facts and figures designed to impress us with the vastness of the oceans. The oceans are indeed vast, comprising some 300 million cubic miles of sea water. However, as N.W. Rakestraw (1951) points out, "It is, in reality, scarcely more than a film of moisture", when one considers the total amount of material in the world. It is, obviously, a matter of perspective.

The total marine fish biomass must also be a figure of such size as to stagger the imagination. However, we have the required sieves to harvest at least part of that resource. These sieves are in the shape of such tools as otter trawls, gill nets, and purse seines. We have one further, but very important, factor in our favor. Fishes are not randomly distributed as are the atoms of gold. Most of them are, to some degree, concentrated by their hydrographic climate, by geography, and by social behavior (Fleming and Laevastu, 1956). A significant part of the total resource still may be so thinly scattered that it is like the gold, not harvestable on any practical basis. We will try to present a case here for suggesting, pending totally new and as yet unforeseen techniques of fishing and marine pisciculture, that there is a limit to the amount of fish that may be harvested each year, that this maximum quantity may be estimated within reasonable limits, and finally, that it is not greatly in excess of what is presently being harvested.

What is being harvested at the present time? Since World War II, various fisheries have developed around the world that have never before been seriously exploited by man. Some of the more recently exploited populations include the tuna stocks of the South Atlantic, the anchovy of Peru and Chile, the sardine of South Africa, and the groundfishes of the Barents Sea. In the last 10 years landings from the oceans have nearly doubled. All of these new fisheries were known to exist as potential fisheries long before they were seriously fished by man. Few such remain, and continued growth at this rate and along these lines cannot be

sticipated. According to the most recent FAO (1960) statistics (Table 1), approximately
[illegible] million metric tons of fish and other related products, both from fresh and salt water,
re landed in 1959. Of this total, marine fin fishes accounted for about 27 million metric
ns.

The clupeoids contribute the largest share, in excess of 11 million metric tons. These
shes are usually taken with purse seines or in traps and weirs. Included in this group are
e herrings, sardines, menhaden, and anchovies. It should be noted that some of these species,
part or entirely, are not directly used for human food. The menhaden, for example, is taken
part for its oil which finds its way into many products other than foodstuffs. Sardines and
chovies largely support the fish meal industry.

The next largest contribution is made by the groundfish species and amounts to more than
million metric tons. These are the species that typically inhabit the great offshore fishing
nks, such as the Grand Bank of Newfoundland, and are fished, for the most part, with otter
awls. The most famous of these fishes is, perhaps, the Atlantic cod.

The jacks, mullets, and sea basses, a most heterogenous group from a taxonomic and fisheries
ewpoint, are recognized as a group for the purpose of landing statistics by the FAO. As such
ey contribute nearly 5 million metric tons to the annual landings.

Tuna landings amount to slightly less than 2.7 million metric tons a year and flounder
ndings to slightly more than 1 million metric tons.

The important fisheries of the world are, without exception, associated either with the
ntinental shelf or with areas of regular hydrographic disturbance, such as upwelling or of
xing of great oceanic currents. Quite obviously the reason for this goes back to the relative
ccess of the plants in these areas. These are the areas where, as Sverdrup (1952) says,
"he oceans plow themselves".

Over the entire globe there are approximately 6×10^9 acres of potentially productive
ntinental areas. Without making any special allowances for differential latitudinal effects,
at might we expect eventually to harvest from this area?

In Tables 2 and 3 we have tabulated the results of some calculations made on the yearly
rvest of demersal species (gadids, hakes, flounders, etc.) from the continental shelf area
the Northwest Atlantic. This area, shown in Figure 1, has been divided into 4 sub-areas
cilitate using the available fishery statistics.

The harvest levels of demersal species, from 7.7 to 12.7 pounds per acre, are surprisingly
milar. The northernmost three areas are intensively fished by vessels from many countries.
ile it is not generally believed that they are necessarily overfished, neither is it apparent
at production can be markedly increased. The demersal species of the Middle Atlantic area
e probably not yet fully exploited, and accordingly the harvest rate is low compared with
at of the other three areas. The pelagic harvest rates, on the other hand, vary extremely,
om 0.2 to 54.2 pounds per acre. There is an interesting increase in harvest of pelagic
ecies southward in this region. This is due to the increased abundance of harvestable
lagic species, the menhaden accounting for the increase in Gulf of Maine and Middle Atlantic
eas.

Similar harvest figures were calculated for areas in European waters. These are presented
Table 4. Although there is more variation in the harvest of demersal species from area to
ea, the values are, on the whole, similar to those obtained for the western Atlantic.

The fishing banks of the North Atlantic are among the more productive in the world and
ve been exploited for centuries. Although the harvest has increased a little in recent years,
can say that in general the fisheries have stabilized, at least for certain species. Although
nagement measures will prevent overexploitation and may result in some increase in harvest,
cannot expect the harvest of these species from these banks to increase by any great percentage.

For purposes of computing the possible world harvest from all continental shelves, we can use
e values for North Atlantic banks. Let us pick 20 pounds per acre as a conservative average
gure. On this basis, the total continental shelf yield would be 120 billion pounds or 55 million
tric tons per year.

To this might be added some poundage of pelagic fish taken in areas remote from land. This harvest is not expected to be large. Even though some tuna fisheries are prosecuted in the equatorial regions of disturbed hydrographic conditions, many of the tuna fisheries are associat with the continental shelf and the yields are properly assigned to the figures computed above.

Thus, we can say on the basis of these calculations that we may, at best possibly double present world harvest of marine fishes. This is assuming, of course, that the fish on all parts of the continental shelf will be as available and as economical to harvest as those of the North Atlantic banks.

We can arrive at another estimate of potential world harvest of marine fishes by an indepen more theoretical technique. This technique, which has been used by Kesteven and Holt (1955), is based upon our knowledge of the primary organic production in the sea and its relation to the production of fish usable by man. Many assumptions regarding the food chain in the sea are involved, but none of these do violence to the beliefs of modern ecologists (Odum, 1959, p. 78). The first of these is that herbivores are 20 percent efficient and each following link in the (carnivore) food chain is approximately 10 percent efficient. The second is that the average marine fish is a second level carnivore. The third is that the net production at each trophic level is fully available to each succeeding level.

For these calculations we begin with an estimate of the net primary production of all oceans. Nielsen (1960) has recently summarized the literature on this subject and has estimated the average annual gross primary production to be between 55 and 70 gm. c/m^2, and the total net production about 1.2 to 1.5 x 10^{10} tons of carbon.

Multiplying by 37 (to convert from grams of carbon to wet plankton weight: conversion factor from Sverdrup, 1946, p. 929, table 101), we may obtain the net amount of phytoplankton produced each year: (1.2-1.5 x 10^{10}) x 37 = 44.5-55.5 x 10^{10}. We will use the average value of 50 x 10^{10}. Assuming that the herbivores (zooplankton) fully harvest this net production and are 20 percent efficient: (50 x 10^{10}) x 0.20 = 10.0 x 10^{10} tons of herbivores (zooplankton). Primary carnivore production at an efficiency of 10 percent is (10.0 x 10^{10}) x 0.10 = 10.0 x 10^{9} tons of primary carnivores, and (10.0 x 10^{9}) x 0.10 = 10.0 x 10^{8} tons of secondary carnivores, marine animals of all descriptions, from which man may take his harvest.

One billion metric tons of secondary carnivores is a very big figure but hardly indicative of what we can expect in the way of bony fishes, even under the best of circumstances. What then is a reasonable figure?

We have calculated on the basis of an ideal system. Some farm fish ponds have nearly reache the levels of efficiency used in the calculations. Odum, op. cit., p. 79 states that "... it is evident that only in the intensively managed German and Oriental fish ponds is a harvest even approaching 10 percent of gross primary production obtained.". On the other hand, few if any natural situations have been found that even remotely approach these various levels of productio individually or collectively.

Evidence that energy is shunted away at various production levels is observed in the bottom deposits of the oceans. There are many types of "oozes" composed largely of the remains of different kinds of organisms. Typical of these are the "diatomacetous" oozes of the North Pacif and around the Antarctic Continent, the "pteropod" oozes of the Atlantic basins and the widespre "globigerina" oozes found in all oceans. Other evidence of sidetracked production may be seen i various fossil deposits, notably the petroleum deposits.

If we assume that in the marine situation 70 percent of the theoretical energy transfer is actively attained at all levels, our estimated annual production of secondary carnivores is approximately 343 million metric tons. Included in this figure, in addition to the marine fishes in which we are principally interested, are many other marine animals such as squids, whales, and sharks, which we conservatively estimate make up 1/3 of the consuming biomass at this and higher consumer levels. All things considered, then, perhaps as much as 230 million metric tons of marine bony fishes are produced on an annual basis. Obviously, however, this quantity cannot be harvested annually without jeopardizing the resource's ability to renew itself. Properly harvested, it is reasonable to suggest that resources of this nature may yield 50 percent by weight, at least, of the net annual production.

We estimate finally, therefore, that perhaps as much as 115 million metric tons of marine fishes may be available for harvest each year. A significant part of this resource is thinly scattered, like the gold, but our fishery technology will have to be greatly improved before a harvest of this magnitude is possible or feasible.

Clearly lacking from the marine environment as significant entities are the efficient erbivorous fishes and for good reason. Marine plant populations are not characterized by their tability; they are subject to violent fluctuations in abundance, the well known plankton blooms, he degree of which depends upon the nature and source of nutrients. These nutrients are seldom ontinuously present and one or more of them, e.g. iron (Menzel and Ryther, 1960), are frequently n such short supply that production rates over a fair proportion of the oceans do not exceed hose of semi-arid grasslands.

The distribution of areas of comparable net primary productivity is shown in Figure 2. It s worth noting that mid-ocean areas are generally unproductive, while the higher latitudes, both orth and south, are exceedingly productive. The reasons for this have been amply and well xplained by Sverdrup (op. cit.). We are concerned with this differential distribution of plant roduction because it qualifies our estimate, given earlier, for the practical expectation of arvest from the continental shelves. Except in certain well known areas where upwelling occurs s, for example, off the west coast of Africa, South and North America, the continental shelf reas of the low and mid-latitudes are characterized by only moderate levels of primary production. n the other hand, most of those areas of shelf characterized by high levels of primary production re already heavily fished. Accordingly, we feel our first estimate of potential groundfish arvest on the continental shelf to be, if anything, too high.

With reference to the various harvest rates listed in Tables 3 and 4, we feel that the ifferences shown are probably quite real. Moiseev (in UNESCO, 1955) lists the biomass of the enthos in a number of seas. A comparison of these data is possible with three of the areas or which we have computed fish harvest rates (Table 5). Some relationship is strongly implied nd, of course, gives us greater confidence in our fish yield figures.

The relation between the benthic biomass and catch per acre has the broadest of implications. he benthic biomass decreases even faster, as one moves offshore, than does the plankton of the hotic zone. According to Zenkevich (UN, 1956), in his discussion of the research done in the orthwest Pacific area, the benthos decreases two to three thousand times in quantity from the ittoral zone to the central parts of the ocean. Under these circumstances, one cannot expect o find any substantial fish population on the bottom beyond the continental slope.

To summarize, it seems reasonable to suggest that although man has not yet fully exploited he marine fish resources it is not so vast as some have been lead to believe. Pending the levelopment of totally new fishing gear and feasible marine pisciculture techniques, such as control of species composition, management of harvest, and fertilization to raise the standing crops, considerably less than 60 million metric tons of marine fishes are available for harvest n an annual basis.

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Table 1. --Present landings of marine fish in millions of metric tons. An estimate based, in part, on FAO statistics for 1959

Species groups	Millions of metric tons
Salmons	0. 9
Flounders	1. 2
Groundfish	6. 2
Clupeoids	11. 4
Tunas	2. 7
Jacks and mullets	4. 9
Sharks and rays	0. 5
Total fin fish	27. 8

Table 2. --Demersal and pelagic species landed from continental shelf of Northwest Atlantic each year, in millions of pounds. Data based on an average of statistics available for years 1956 through 1958

Location	Demersal	Pelagic	Total
Grand Bank	1, 226	18	1, 244
Nova Scotia	835	215	1, 050
Gulf of Maine	584	216	800
Middle Atlantic	146	1, 029	1, 175

Table 3. --Catch in pounds/acre/year from the continental shelf of the Northwest Atlantic

Location	Demersal	Pelagic	Total
Grand Bank	11.8	0.2	12.0
Nova Scotia	10.8	2.8	13.6
Gulf of Maine	12.7	4.7	17.4
Middle Atlantic	7.7	54.2	61.9

Table 4. --Catch in pounds/acre of various well known fishing areas. Computations by authors based on statistics from several sources

Location	Period	Demersal	Pelagic	Total
North Sea	1956-58	10.0	16.6	26.6
Baltic	1956-58	4.1	3.5	7.8
Barents Sea	1956-58	15.7	0.8	16.5
Iceland Banks	1956-58	29.0	5.3	34.3
Adriatic[1/]	1947-53	2.5	2.1	4.6

1/The Adriatic is generally considered to be overfished.

Table 5. --A comparison of fish yields with amount of benthos

Location	Biomass of benthos (g/m^2)	Pounds/acre fish (1956-58)
North Sea	244	26.6
Baltic Sea	33	7.6
Barents Sea	100	16.5

Figure 1. --The continental shelf of the Northwest Atlantic showing four areas referred to in the text.

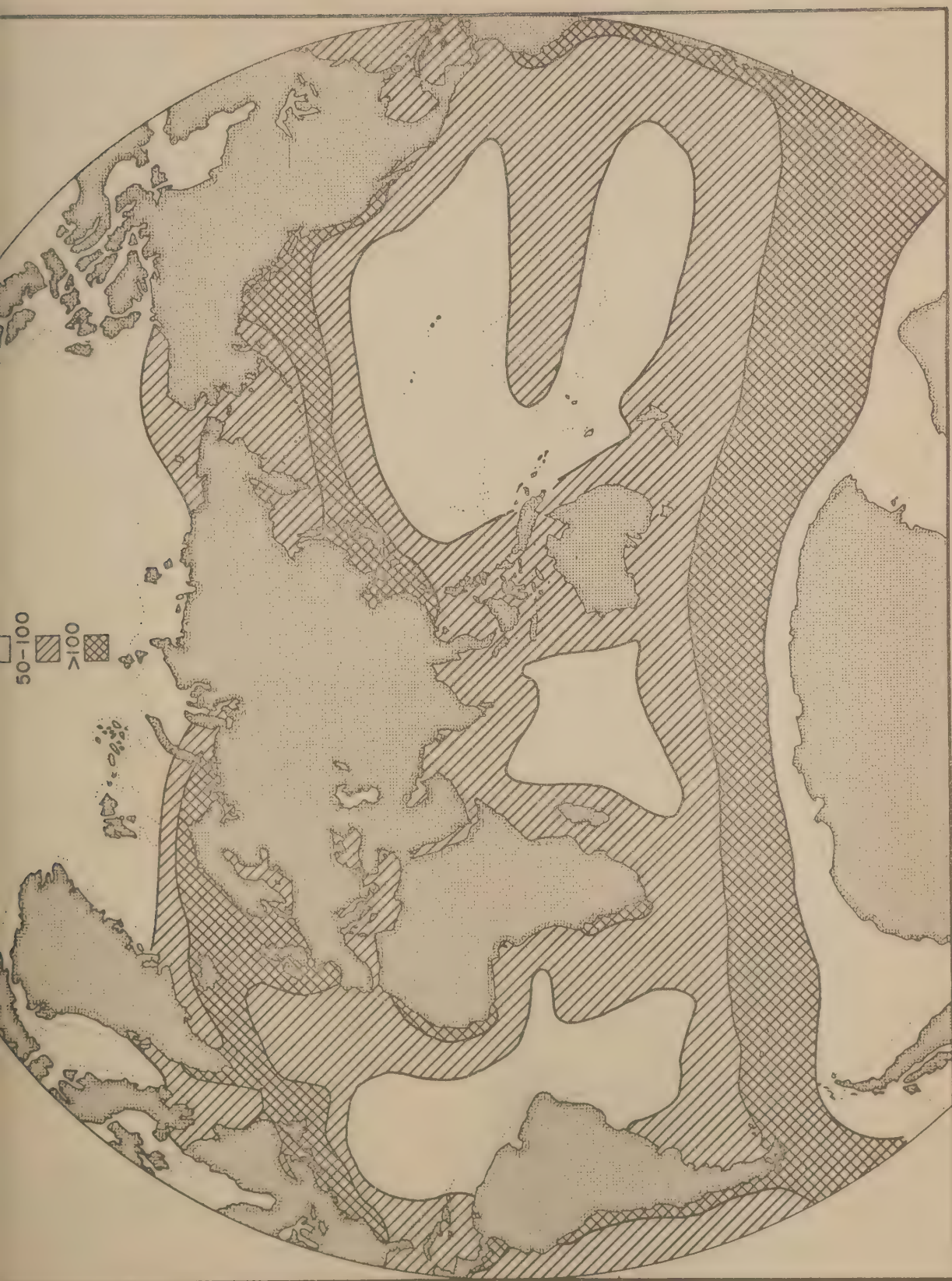

Figure 2.--Generalized chart of net primary production.

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Predation of Bluefish on Young Atlantic Menhaden in Indian River, Delaware

ABSTRACT

**ach contents of 262 bluefish, *Pomatomus*
, were examined to determine whether
cies is predatory on young Atlantic men-
Brevoortia tyrannus. Food occurred in 209
s, of which 90 per cent contained fish and
cent contained invertebrates. Silversides
first both in frequency of occurrence (46
s) and in the number consumed (105).
en occurred in 39 stomachs (19 per cent of
achs which contained food), and a total of
aden had been consumed for an average
r bluefish examined.**

e search for sources of mortality on young menhaden, *Brevoortia tyrannus*, in es- nurseries, the role of predators must be ed. Bigelow and Schroeder (1953:115), (1948:132), Goode (1879:106), U. S. Fish and Fisheries (1873:246), and others hat bluefish, *Pomatomus saltatrix*, were the chief enemies of menhaden, but few of their food habits were reported. Since occur in many estuaries along the Atlantic the United States (Bigelow and Schroe- d.:384; U. S. Comm. Fish and Fisheries,), generally from May through September, val and juvenile menhaden, it is of pri- terest to determine whether young men- re an important item in the bluefish diet. esent study summarizes the results of analysis of bluefish collected in Indian Delaware during the summers of 1956, 1957, 8. The data were obtained during studies ed with determining the factors affecting ribution and abundance of young men- this locality.

les totalling 262 bluefish, ranging from 34 nm fork length (Fig. 1), were caught with eines, plankton nets, and gillnets and pre- n 10 per cent formalin. Forty-three speci- ere collected in 1956, 25 in 1957, and 194 Food organisms were removed from the s, identified, and the number and/or vol- each kind of organism determined. In some was necessary to estimate the volume of ms because of their small size. Stomach of fish collected in different years were and the results were combined (Table 1).

e 262 stomachs examined, 209 (80 per cent) d food items, 42 (16 per cent) were empty, (4 per cent) contained mud and plant de- those containing food, 90 per cent con- fish, and 14 per cent contained inverte- Fish accounted for 98 per cent of the e volume of contents, and only five spe- luding menhaden, bay anchovy (*Anchoa*), mummichog (*Fundulus heteroclitus*), and Atlantic and tidewater silversides (*Menidia menidia* and *M. beryllina*) accounted for 86 per cent of the aggregate volume. Of these, silversides ranked first in frequency of occurrence and were consumed in the greatest number (105); mummichog accounted for the greatest share of the total food volume (65 per cent). An unidentified polychaete and opossum shrimp (*Neomysis americana*) were the most common invertebrates.

There was an increase in average volume of food per stomach with an increase in bluefish length; the average volume ranged from 0.9 cc in the 30–49 mm size group to 25 cc in the 170–189 mm size group. Invertebrates accounted for 24 per cent by volume of the food specimens smaller than 70 mm, whereas, fish constituted almost 100 per cent of the food of those larger than 90 mm. These findings are in contrast to a statement by Bigelow and Schroeder (1953:384) that "...young 'snappers', 6 to 8 inches long [150 to 200 mm.], feed largely on copepods, or crustacean and molluskan larvae, as well as on fish fry smaller than themselves."

Menhaden in various stages of digestion were found in 39 stomachs (19 per cent of the stomachs which contained food). A total of 46 menhaden found in the stomachs represented an average of 1.2 per bluefish, or about 0.2 menhaden for all bluefish examined; three were the most found in any one stomach. Fig. 1 shows that bluefish of nearly all sizes had fed on young menhaden and in about the same proportion over the size range represented. Lengths of menhaden found in the stomachs (Table 2) indicated that the larger bluefish fed upon larger menhaden; the smaller bluefish ingested menhaden which were more than one-half their length.

It is concluded that young menhaden were one of the more important foods of bluefish in Indian River, but what effect such predation may have

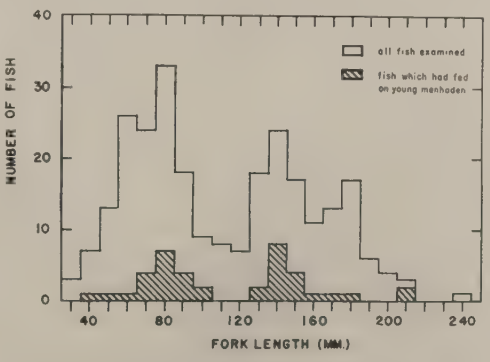

Fig. 1.—Length frequencies of bluefish, *Pomatomus saltatrix*, examined and those which fed on young Atlantic menhaden, *Brevoortia tyrannus*.

on the abundance of young menhaden in relation to other factors in this estuary needs further investigation.

TABLE 1.—Stomach contents of bluefish, *Pomatomus saltatrix*, taken from Indian River, Delaware, 1956–1958.

Item	Number of organisms	Stomachs in which food item occurred		Aggregate volume	
		Number	Per cent	Cubic centimeters	Per cent
Annelids:					
Unidentified polychaetes	28	17	8.1	1.0	0.6
Crustaceans:					
Lerneaenicus sp.	3	2	1.0	0.1	0.1
Unidentified copepods	ca. 200	2	1.0	0.1	0.1
Unidentified amphipods	4	2	1.0	0.1	0.1
Neomysis americana	ca. 170	11	5.3	0.6	0.4
Callinectes sapidus	1	1	0.5	1.2	0.7
Unidentified decapods	4	2	1.0	—	—
Fishes:					
Brevoortia tyrannus	46	39	18.7	25.5	15.8
Anchoa sp.	2	2	1.0	—	—
A. mitchilli	32	9	4.3	13.1	8.1
Anguilla rostrata	1	1	0.5	0.1	0.1
Cyprinodon variegatus	12	6	2.9	1.9	1.2
Lucania parva	6	5	2.4	2.1	1.3
Fundulus sp.	1	1	0.5	0.1	0.1
F. heteroclitus	55	27	12.9	65.4	40.5
F. majalis	1	1	0.5	0.1	0.1
Mugil curema	1	1	0.5	—	—
Menidia sp.	84	34	16.3	22.4	13.9
M. beryllina	6	3	1.4	3.2	2.0
M. menidia	15	9	4.3	9.2	5.7
Microgobius thalassinus	4	1	0.5	2.0	1.2
Unidentified fish	74	71	34.0	13.1	8.1
Unidentified animal remains	—	8	3.8	0.3	0.2

TABLE 2.—Lengths of Atlantic menhaden *voortia tyrannus*, ingested by bluefish, *tomus saltatrix*, of different lengths

Fork length of bluefish (millimeters)	Fork length of menh (millimeters)
49	27
56	29
72	45
72	38
89	40[1]
140	50[1]
144	40[1]
147	45
147	50
149	50[1]
149	50[1]
150	50
152	51
163	60
177	85
181	90[1]
213	70

[1] Lengths are approximate because of digestion of the caudal fin.

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Sexual Dimorphism in Oyster Drills of Chincoteague Bay, Maryland-Virginia

ABSTRACT

The sex and length of 5,475 oyster drills, *Urosalpinx cinerea follyensis* and *Eupleura caudata etterae*, were determined to ascertain if a significant difference exists in the mean size of males and females. The mean length of female *U. cinerea* was 28 mm, and of males, 24 mm; of female *E. caudata*, 29 mm, and of males, 25 mm. Statistical treatment of the data indicates that females of both gastropod species are significantly larger than males.

Investigations of the diecious gastropods *Urosalpinx cinerea* (Say) and *Eupleura caudata* (Say) family Muricidae, Subclass Prosobranchia) have shown that females of these species attain a greater maximum height than males (Federighi, 1931:86; Hale, 1942:490; Stauber in Carriker, 1955:26–7; Hargis and MacKenzie 1961:9 & 12). Federighi reported that of the individuals of *U. cinerea* collected in Chesapeake Bay the largest male was 33 mm and the largest female was 33 mm in shell height. Cole did not find a significant number of males of this species higher than 36 mm, whereas the females ranged as high as 43 mm. No further statistical evidence has been presented to support these observations. This paper reports the results of a quantitative study of the differences in maximum height of male and female *Urosalpinx cinerea follyensis* and *Eupleura caudata etterae* (Baker, 1955:73–6) in Chincoteague Bay, Maryland and Virginia, in the summers of 1958 and 1959.

Of a total of 6,320 drills collected and examined, 5,482 were removed from oyster drill traps of the type described by Galtsoff et al. (1937) and 1,138 were collected by hand from the bottom of the bay by a diver wearing SCUBA equipment. It was possible to determine accurately the sex of 4,675 animals; the remaining 845 drills were juveniles and did not possess the definitive sex characters used.

Sex of the gastropods was determined by examination of the genitalia, exposed by crushing the shell, under a magnification of three powers. Genitalia were described by Federighi (1931:101), Fretter (1941:182), and Hargis (personal communication). In many cases a small vestigal structure resembling the penis was also seen in females. Confirmation of the sex in such cases was made by research for the egg capsule gland, sperm ingesting gland, and ovary, all easily identified organs characteristic only of females.

Drills in the sample ranged in height from 2 mm to 45 mm. Snails smaller than 17 mm were generally immature. Since it was difficult or impossible to determine their sex, they were not considered in this study. However, many animals smaller than this displayed distinctive sex characters.

Of the 3,942 individuals of *U. cinerea* sexed, 2,196 were females and 1,746 were males. The females possessed a mean height of 28 mm and the males a mean height of 24 mm. Of the total number of females sexed, 269 or 12.2% were 35 mm in height or over, and only 20 males, 1.1%, were in this height range (Fig. 1).

The sex of 1,533 individuals of *E. caudata* was also determined. This group contained 883 females and 650 males. The mean height of the females was 29 mm and that of the males was 25 mm. Of the 883 females, 403, constituting 45.6%, were 30 mm in height or more. Only 28 of the 650 males, constituting 4.3%, were higher than 30 mm (Fig. 2).

The sex ratio of the number of males to females of all animals examined was 1:1.3 for *U. cinerea* and 1:1.4 for *E. caudata*. There was some variation in ratios of trapped and hand collected drills. The male to female ratio of trapped *E. caudata* was 1:1.6 and ratio of hand collected animals was 1:1.2. The greatest variation occurred in the ratios of *U. cinerea*. Trapped *U. cinerea* showed a sex ratio of 1:1.3 and the ratio of hand collected animals was 1:0.8. However, it should be pointed out that there was a large difference in the number of

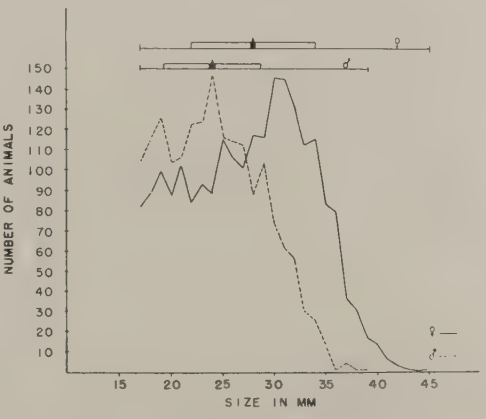

Fig. 1.—Length-frequency and size distribution of the gastropod *Urosalpinx cinerea* from Chincoteague Bay. The lower figure (curves) represents the length-frequency of the sexes. The upper figure represents the size distribution of the sexes. In the upper figure the single horizontal line represents the size range. Two standard errors on either side of the mean (vertical bar) are shown as the black bar and one standard deviation on either side of the mean is depicted by the white bar.

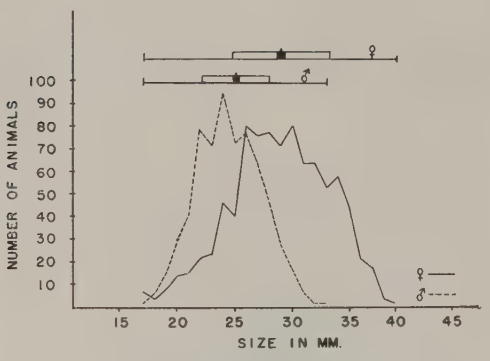

Fig. 2.—Length-frequency and size distribution of the gastropod *Eupleura caudata* from Chincoteague Bay. The lower figure (curves) represents the length-frequency of the sexes. The upper figure represents the size distribution of the sexes. In the upper figure the single horizontal line represents the size range. Two standard errors on either side of the mean (vertical bar) are shown as the black bar and one standard deviation on either side of the mean is depicted by the white bar.

trapped and hand collected *U. cinerea*; of the 3,942 individuals collected for this study only 366 were gathered by hand.

Standard deviation and standard error of the mean were calculated for height of both populations of *U. cinerea* and *E. caudata*. Standard deviation was 6.1 mm and standard error of the mean was 0.13 mm for the height of the females of *U. cinerea*. For male *U. cinerea* a standard deviation of 4.6 mm and a standard error of the mean of 0.11 mm was found. Corresponding calculations for *E. caudata* gives a standard deviation of 4.3 mm and a standard error of the mean of 0.15 mm for females and a standard deviation of 2.9 mm and a standard error of the mean of 0.11 mm for males. Graphic comparison of the samples in the manner described by Hubbs and Hubbs (1953:49–57) indicated that females of both species were sig cantly larger than males (Figs. 1 and 2).

In conclusion, a plot of the length-freque distribution of individuals of both *U. cinerea E. caudata* (Figs. 1 and 2) indicates further females in these samples were larger than m and that the differences in the mean heights significant.

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Survival and Behavior of Sockeye Salmon Fry Migrating into Brooks Lake, Alaska

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ABSTRACT

This paper describes the behavior of sockeye salmon fry (*Oncorhynchus nerka*) during their migration from stream spawning gravels to lake nursery areas. Fry were negatively phototactic, sought holding areas along stream banks during daylight hours, and only left holding areas and gravel to migrate during the darkest hours of the night. Fry migrated as individuals, facing downstream, and usually exhibited swimming movements. Certain features of the migratory behavior are discussed in terms of survival values in the face of intense piscivorous predation.

INTRODUCTION

As they emerge from stream spawning ravels and migrate to lake nursery areas, ockeye salmon fry (*Oncorhynchus nerka*) re highly vulnerable to piscivorous predators oth in the streams and in the lakes around ie stream mouths. A migratory behavior attern has surely been developed with pecific survival values.

Year-round research on the freshwater ife history of sockeye salmon is carried on by ie U. S. Bureau of Commercial Fisheries at s field station at Brooks Lake, Alaska. This aper reports field observations on the migra- ory behavior of sockeye salmon fry at Hidden reek in the spring of 1960. This small spawn- ng tributary drains into Brooks Lake, which n turn drains into Naknek Lake and eventu- lly Bristol Bay (Figure 1).

Previous studies on behavior of Pacific almon fry dealt primarily with the seaward igration of pink (*O. gorbuscha*) and chum *O. keta*) salmon fry. Hoar (1951, 1953, 954, and 1956) observed their behavior in quaria, tanks, and troughs. Neave (1955) nade some valuable field observations on ewly emerged pink and chum salmon fry uring their migration to nursery areas.

Hoar (1954) gives some information on he behavior of sockeye salmon fry and smolt n his laboratory. Since his observations were nade under artificial conditions, he cautions that ". . .it remains for the ecologists to show how these ethological experiments are related to the activities of young salmon in their native surroundings."

McDonald (1960) recently published observations on Pacific salmon fry migrating at Lakelse Lake, British Columbia. His observations on sockeye salmon fry are pertinent to our study.

FRY TRAPPING AND ENVIRONMENTAL FACTORS

Sockeye salmon fry were trapped as they migrated from Hidden Creek to determine the percentage survival of eggs carried into Hidden Creek by the parent stock. The observations on migratory behavior of fry reported in this paper were made during this trapping operation.

Hidden Creek is about 2 miles long and drains a series of beaver ponds. It averages 1 foot in depth, 10 feet in width, and has a flow of 10 to 20 cubic feet per second. The water is usually clear. Adult sockeye salmon spawn throughout the 2 miles of creek.

The 1960 spring fry outmigration was inventoried near the creek's mouth where the stream was divided into two trapping sites of equal width. A fine-mesh nylon fyke net was used to trap fry at each site. It had 4-foot wings and a 4-inch-square funnel opening. Fine-mesh wire screening was used to divide

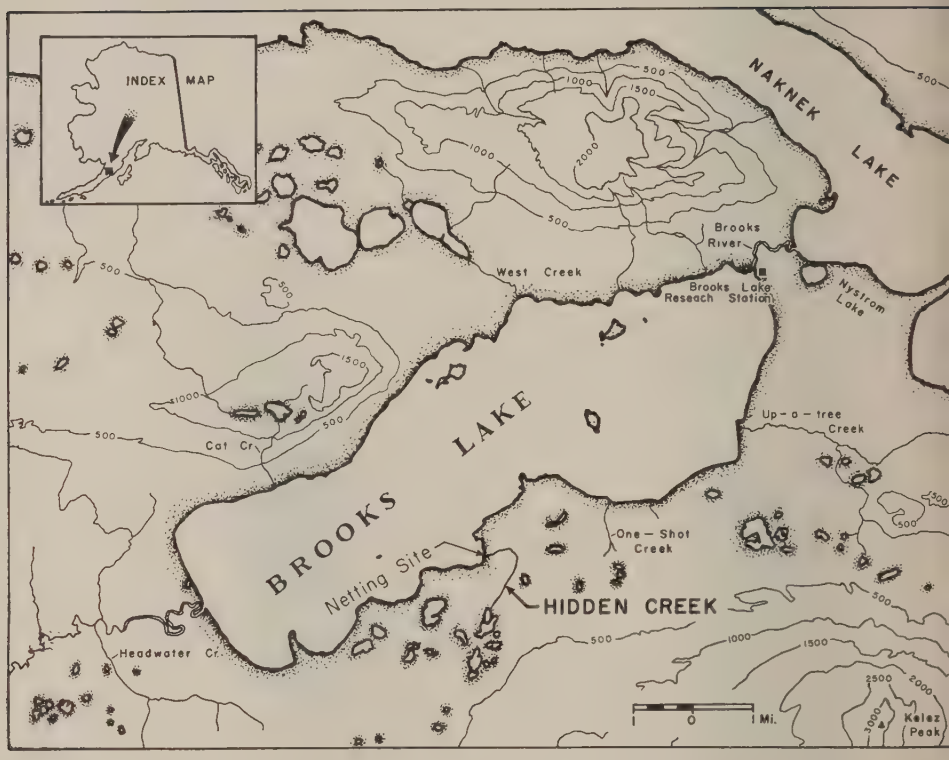

FIGURE 1.—Location of Brooks Lake laboratory and Hidden Creek, sockeye salmon spawning tributary Brooks Lake, Alaska.

the two sites and to lead from the net wings to shore.

The net was alternated hourly between sites from 8 p.m. to 4 a.m. each night. Initial fishing sites were alternated each night. At the end of 55 minutes of fishing, the net was emptied and then set in the other site. All fry were counted and released downstream from the fishing site.

Fry were counted individually in small catches and by fives in large catches. Counting by fives was evaluated by recounting 30 samples carefully by ones. The difference between counts by fives and counts by ones averaged less than 1 percent, and no adjustments of catch data were made for counting by fives.

Water temperatures and incident solar radiation were measured. A pocket field thermometer was used to measure water temperatures hourly in Hidden Creek. A constant recording pyrheliometer located at the Brooks Lake field station was used to measure incident solar radiation 24 hours a day. The instrument was located 6.6 miles fr Hidden Creek, and the recordings are c sidered representative for the creek.

HIDDEN CREEK FRY OUTMIGRATION

Adjustments of catch data

Catches of sockeye salmon fry from Hid Creek require certain adjustments bef estimating the outmigration.

The first consideration is the relative cat ability of the two sites. The dividing lea placed in midstream quite closely split outmigration in half. During the period the total spring outmigration where compa tive data are available (25 nights), 151, fry or 52.6 percent of the total catch (28 372) were caught at one site, and 136,659 or 47.4 percent of the total were caught the other. Thus, the alternate hourly catch each site is doubled to estimate the nigh and seasonal outmigrations.

Since 5 minutes of every fishing hour w required to pull the net, empty the catch, a

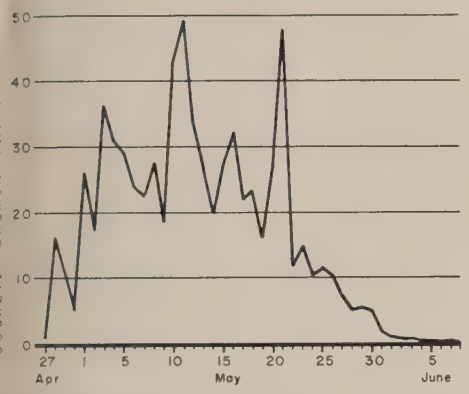

FIGURE 2.—Nightly sockeye salmon fry outmigration from Hidden Creek, spring 1960.

eset the net, estimates of the outmigration ere multiplied by 12/11 or 109 percent for djustment.

An adjustment of the daytime outmigration s the final consideration of the estimation. Complete 24-hour catch data from midnight o midnight were obtained April 29 and May , 9, and 11. Virtually all of the catch, 54,199 ut of 55,988 fry or 97.9 percent, was taken etween midnight and 4 a.m. and between p.m. and midnight. On several other days, ishing a net for several hours before or after he standard 8 p.m. to 4 a.m. fishing period esulted in a negligible catch. Finally, catches uring the standard fishing period were egligible during the first and last hours. It ppears that the standard fishing period of 8 .m. to 4 a.m. furnishes an estimate that losely approximates the actual total outmigraion over the 24-hour period.

All references to the fry outmigration that ollow will refer to adjusted catches. Adjustents usually required doubling the catch and hen multiplying by 109 percent. Whenever net was fished overnight in one site, the adustment merely involved multiplying the atch in one site by 100.0/52.6 or the catch in he other site by 100.0/47.4. During the last ew days of the outmigration, onshore waves lisarranged one site so that it was purposely losed by fine-mesh plastic screen, and the ntire outmigration passed through the other ite. Adjustment of these catches merely required multiplying by 109 percent.

Outmigration and survival

Fry outmigrations from Hidden Creek for ach night in the spring of 1960 are plotted in Figure 2. Fry started to emerge from Hidden Creek about April 25. Only a few fry were seen in sheltered areas along the lower 100 yards of the creek. They were more numerous by April 27 when the net was first set, and numbered in the hundreds in these areas during the major portion of the spring outmigration. The outmigration dwindled in early June. Trapping was terminated June 9, and by June 13, no fry could be seen in the sheltered areas.

TABLE 1.—*Vital statistics for determining survival to migrant fry stage of 1960 adult stock of sockeye salmon in Hidden Creek, Alaska*

Item	Value
Adult stock	4,558 fish
Adult sample	692 fish
Females in sample	351 or 50.7%
Females est. in adult stock	2,301 females
Average mid-eye fork length of females	53.92 cm
Average fecundity[1]	3,725 eggs
Potential egg deposition of adult stock	8,571,225 eggs
Fry outmigration	726,896 fry
Survival	8.5%

[1] Based on length–fecundity relationship derived from total count of eggs in 25 females in 1959.

The estimated spring fry outmigration was 726,896, which represents 8.5 percent survival of the potential egg deposition (Table 1).

Hourly migrations between 8 p.m. and 4 a.m. are shown for the 37 nights from April 28 through June 4, excepting May 13 (Figure 3). Rough water that evening prevented the biologist from returning to Hidden Creek from the main camp.

Hourly migrations overnight followed a dome-shaped pattern. Very few fry migrated in the earliest and latest hours. The peak or peaks were between 10 p.m. and 1 a.m. This pattern was repeated every night throughout the spring outmigration when fry were sampled hourly (Figure 3).

Environmental influences

Two environmental factors, water temperature and light, were studied in relation to the outmigration pattern.

Water temperatures cannot be correlated with the pattern of nightly migration. For example, on April 29 the water temperature dropped only 1° F. between 8 p.m. and 4 a.m. On May 21 the water temperature rose 1° F. between 8 p.m. and 4 a.m. The greatest drop over the time period was 8° F., recorded the night of May 28. The usual drop in water temperature between 8 p.m. and 4 a.m. was 2° to 3° F. Still the pattern of nightly migration remained similar on all nights.

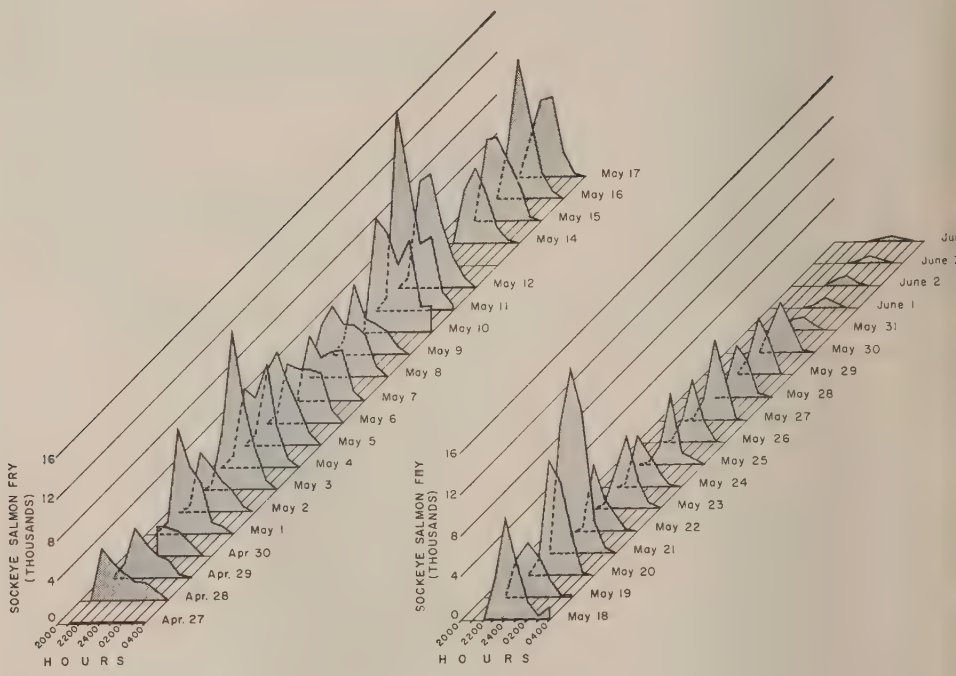

FIGURE 3.—Sockeye salmon fry outmigration at Hidden Creek, spring 1960.

Light appears to be the most important environmental factor influencing the migratory behavior of pink and chum salmon fry (Neave, 1955, and Hoar, 1956). Light also strongly influences the natural migratory behavior of sockeye salmon fry.

Comparing the hourly migration patterns (Figure 3) with pyrheliometer records for four 3-day periods revealed three salient features. First, fry did not start migrating until after dusk and they stopped before dawn; second, peak outmigrations occurred during the darkest hours of the night; and third, the outmigration pattern narrowed and became increasingly confined to the darkest hours as dusk became later and dawn earlier in the spring.

It appears that the nightly migration mode also shifted during the seasonal increase in the daylight period. It shifted roughly from 11 p.m. in late April to 12 p.m. in late May. These features of migration compare closely with those found by McDonald (1960) for sockeye salmon fry at Lakelse Lake, British Columbia.

Hidden Creek water remained clear during the spring outmigration, presenting no opportunity to view the effects of turbid wa on fry migration. Neave (1955) states t pink and chum salmon fry do migrate dur daylight in highly turbid waters.

FRY BEHAVIOR

While fry were being enumerated, the portunity frequently arose to observe th behavior. These observations are summari here and lend an insight into the survi value of the natural migratory behavior sockeye salmon fry at Hidden Creek.

Holding areas

Sockeye salmon fry accumulate and hold stream side areas during the spring emerger Such areas are usually in irregularities in stream banks associated with clumps of v etation hanging out into the creek. Emerg fry use the same holding areas day after d The lower 100 yards of Hidden Creek cont many such areas, and hundreds of fry occu them in the daytime during most of the spr outmigration.

In daylight hours fry could be scared fr a holding area, but they soon returned to same area or to the next one downstream.

variably remained in the top 6 inches of ater where vegetation was most dense. They ormally maintained their position facing into e current.

Holding areas were evacuated during ghtly outmigrations. Few fry were ever seen them during the migration peaks between p.m. and 1 a.m. As dawn came, however, y would again begin to accumulate in the lding areas. Evacuation of one holding ea was viewed from 9:15 p.m. to 1:10 a.m. e night of May 30. The holding group, hich initially consisted of about 45 fry, re- ained virtually intact through 10:20 p.m., as reduced to about 33 fry by 10:50 p.m., about 18 by 11:30 p.m., and to 2 by mid- ght. This area was completely evacuated by 10 a.m. During the periodic observations, ve fry were seen leaving the group singly, id two were seen leaving together.

Stream movements

Quantitative observations of migrating fry er a white background panel or sandy bot- m were made with a carefully shielded gas- ine lantern on 11 occasions. Sockeye lmon fry migrated out of Hidden Creek in- vidually and not in schools. Of the 315 y recorded, 313 were migrating singly with apparent reference in time or space to other dividuals. The remaining two fry were mi- rating together when observed. These ob- rvations agree with those of McDonald 960) for sockeye salmon fry and Neave 955) for pink salmon fry, which also mi- rated singly after emergence.

Sockeye salmon fry did not drift with the rrent facing upstream during the migration Hoar speculated (1954), but rather faced wnstream and actively migrated. Pritchard 944) and Neave (1955) found an identical igrating behavior for pink salmon fry. Only 2 of the 240 sockeye salmon fry recorded for igration direction in Hidden Creek were cing upstream. Two hundred and twenty- ght or 95 percent were facing downstream id were usually swimming faster than the rrent flowed. Fry were often seen wiggling eir bodies and performing swimming move- ents. McDonald (1960) obtained only mited data on orientation during migration id leaves the question open. He did note me instances of sockeye fry swimming down- ream with the current (p. 663).

Lake schooling

Fry behavior appeared to change dramatically after fry entered the lake, although the evidence is only circumstantial. No fry were followed for any length of time after they entered the lake, but whenever fry were observed in the lake, they were schooled. Schools have been observed along the lake perimeter many other times over the past several years, usually in daylight in shallow water. Between 20 and 200 fry make up a school, and each individual within a school acts with reference in both time and space to the other individuals. They travel, turn, take flight, and respond as a highly integrated unit typical of schooling fishes.

Appearance of schooled fry in well-lighted areas denotes a sharp change from negative phototaxis. This change is considered a requisite for schooling and feeding, both functions strongly related to visual stimuli (Neave, 1955; Hoar, 1956; and McDonald, 1960).

Phototaxis and rheotaxis

The response to light and current by salmon fry has been the subject of much experimental research by Hoar (1951, 1954, 1956), McKinnon and Hoar (1953), and others, and the subject of observational research by Neave (1955). The early experimental work furnished information on fry after they had schooled. Neave (1955) pointed out that field observations revealed quite a different behavior pattern among fry before they have schooled. The interpretation of pink and chum salmon fry behavior by Neave (1955) and Hoar (1956) is as follows: (1) Newly emerged fry are negatively phototactic; they avoid strong light and prefer cover during daytime holding periods. (2) Newly emerged fry are negatively rheotactic; migration is effected by swimming downstream in the current. (3) Newly emerged fry act as individuals in migration. (4) At the end of the migration into the nursery areas or after extensive holding, schooling takes place and a dramatic change occurs in pink and chum salmon fry behavior; they show less cover response and generally remain in brightly lighted areas. Hoar (1956) suggests that they now rely on the protection of the school and its associated advantages. They become neutrally or even strongly positively rheotactic.

Hoar (1954) also carried out limited experimental research on sockeye salmon fry.

However, the fry had been trapped and held for a period of time before introduction into the observation chambers. His observations agree with the behavior of sockeye salmon fry once they have reached Brooks Lake and schooled. Apparent disagreement in lake behavior concerns fry preference for deep water that Hoar postulates. Many schools of fry have been observed along the shores of Brooks Lake after the spring emergence, some a half mile or more from spawning tributaries. Thus, some fry at least do not immediately seek deep water after reaching the nursery lake. Regarding stream behavior, Hoar postulated that sockeye salmon fry drifted inactively downstream during migration and were schooled. Such behavior is entirely opposite from that observed in Hidden Creek.

Sockeye salmon fry show a behavior pattern similar to that now recognized for pink and chum salmon fry. Newly emerged fry in Hidden Creek seek the cover of overhanging vegetation during daylight hours. They are negatively phototactic. They migrate by swimming downstream as individuals. Fry reaching the lake after the short migration from Hidden Creek are only seen in schools that act as highly integrated units of individuals, generally remain in brightly lighted areas, and show neutral and sometimes strongly positive rheotaxis.

An interesting observation on the strength of the rheotactic response by one school of fry warrants cautious speculation on the mechanism that confines juvenile sockeye salmon to lake nursery areas until they emigrate as smolts. On June 3, 1960, a school of about 30 fry were seen cruising the lake shore 200 feet away from Brooks Lake outlet. The senior author herded these fry down to within 20 feet of the outlet and then hid on shore. The surface current toward the outlet was quite noticeable as much debris was drifting along in that direction. The fry immediately resumed their lakeshore cruising away from the outlet and into the current. After the fry had proceeded 10 feet or so, they were again herded toward the outlet, this time to within 15 feet. The current was noticeably stronger, and it was more difficult to herd the fry down this far. The senior author hid again, and the fry immediately began to cruise along the shore away from the outlet. The fry were herded toward the outlet a third time to the very brink where the current was quite strong. It was more and more difficult to herd the fry as the brink of the outlet was approached and the current grew stronger. After the fi herding, the fry were in a strong current, they appeared to have considerable diffic in maintaining their positions. After 2 o minutes they sidled over to the shore to edge of the water where the current was we est, and then they cruised up along the sh away from the outlet. Before observati were stopped, they had cruised 50 feet.

These observations show that the rheota response can be extremely powerful. We s gest that this mechanism, developed am fry after schooling, could be the domin factor that confines juvenile sockeye salm to lake nursery areas. When they are re to leave the lake for the ocean as smolts, mechanism must either break down or superseded by some more powerful drive.

Some sockeye salmon spawning grounds located below lake outlets in rivers that l directly to the sea (*e.g.*, Karluk River, A ka). Sockeye salmon fry are often obser in schools during daylight, migrating upstre to the lake nursery area. The value of a str positive rheotactic response and schooling havior among fry in this type of situatio obvious, the only alternative being fry mig tion to the sea, which occasionally happe Apparently schooling and the adaptive chan to positive rheotaxis and loss of negat phototaxis associated with it take place bef the emerging fry reach the sea, or even p haps before they move very far from the r sites.

Another situation of interest when consid ing the final direction of fry migration fr the spawning grounds is as follows. So spawning grounds are in trunk rivers betw lakes (*e.g.*, Brooks River, Alaska). Here, least, fry migrate downstream into the ou nursery area, Naknek Lake. This is the log direction in trunk rivers that empty into s able nursery areas. Of course, in lake tri taries, there is no alternative but to m downstream to the lake.

SURVIVAL VALUE OF MIGRATORY BEHAVIO

The outmigration of sockeye salmon was subject to considerable predatory p sure in and immediately around the mouth Hidden Creek. The most abundant and vo cious predator was the Dolly Varden *Salveli malma*. Predatory rainbow trout, *Sal gairdneri*, juvenile coho salmon, *Oncorh chus kisutch*, and coastrange sculpin *Cot aleuticus*, were present in moderate numbe

Dolly Varden continually fed on fry during
nightly outmigrations. A number were
ken in the fry trap, and 14 were examined
stomach contents. Some had fresh fry,
t most fry were partly or even quite well di-
ted and were probably taken several hours
fore the Dolly Varden were captured and
d access to fry in the net. The 14 Dolly
rden averaged 6.9 inches in fork length.
ur of the stomachs were empty, and one
ntained 89 fry. The average was 32 fry
stomach. Intensive feeding activity in the
eam and around its mouth was observed
roughout each night's migration period.

Dolly Varden predation on sockeye salmon
is commonly reported. Roos (1959) in his
od study of Dolly Varden at Chignik,
aska, found some predation on sockeye
mon fry, but they were a minor diet item.
reported (1960) that juvenile coho salmon
re more serious predators. Roos also re-
ewed some pertinent literature: Semko
956) in studies in the Bolshaya River in
st Kamchatka considered Dolly Varden the
ief predator of sockeye salmon fry. Bower
929) found Dolly Varden feeding to a con-
derable extent (39 percent of the feeding
h) on sockeye salmon fry and fingerlings
the Chignik River. Foerster and Ricker
941) found that the removal of 18,327
edator fish, including 935 Dolly Varden,
om Cultus Lake from 1932 to 1938 mark-
ly increased the survival rates for juvenile
ckeye salmon.

At least three features of the fry migratory
haviour observed in our studies appear to
ve survival values in the face of predatory
essure in Hidden Creek and its mouth.

Fry sought holding areas along the stream
nks during daylight hours. These holding
eas were in or immediately behind clumps
streamside grasses that overhung the water.
ch a cover-seeking behavior has obvious
rvival value in daylight.

Fry left the holding areas and gravel to mi-
ate during the darkest hours of the night.
dden Creek is a shallow, clear-water stream;
would be least vulnerable to predation at
at time.

Finally, fry actively migrated downstream.
tive swimming by migrating fry also could
prove their survival opportunity by achiev-
g rapid transit through the predatory zone.
escape behavior from predatory fish was
served, but fry did take flight when ap-
oached by a man wading.

These features of behavior that have survival values during migration are not limited to sockeye salmon fry at Hidden Creek. In British Columbia, pink and chum salmon fry (Neave, 1955) and sockeye salmon fry (McDonald, 1960) show quite similar behavior patterns.

Such behavior is a logical response to piscivorous predation during migration of small fish from stream spawning gravels to lakes or the ocean. It is reasonable to suspect that further field observations on other salmonids will reveal similar migratory behavior patterns where predatory pressure is or has been intense.

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he Use and Selectivity of Small-Meshed Gill Nets at Brooks Lake, Alaska

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The Use and Selectivity of Small-Meshed Gill Nets at Brooks Lake, Alaska

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ABSTRACT

Fine-thread gill nets with meshes of ⅜-, ½-, ¾-, ⅞-, and 1-inch (stretched measure) were used to sample lake-dwelling juvenile sockeye salmon (*Oncorhynchus nerka*) and associated small fishes in Brooks Lake, Alaska. Thirteen of 20 species known to occur in the lake were sampled with the small meshes. Sockeye salmon, Alaska blackfish (*Dallia pectoralis*), threespine stickleback (*Gasterosteus aculeatus*), ninespine stickleback (*Pungitius pungitius*) and sculpins (*Cottus* spp.) less than 50 millimeters in length were sampled. Different selectivity patterns were shown by different species in various mesh sizes. Meshes smaller than 1 inch had low catch efficiencies, although these meshes were useful for qualitative assessment of small fishes.

INTRODUCTION

Selectivity of gill nets is important when choosing mesh sizes for sampling fish populations. The selectivity of fine-thread experimental gill nets with meshes of ⅜- to 1-inch (stretched measure[1]) was studied during 1957 and 1958 at Brooks Lake, Alaska. Emphasis was on sampling lake-residing juvenile sockeye salmon (*Oncorhynchus nerka*) and associated small fishes.

The selectivity of gill nets and other entanglement gear has been the subject of considerable study, but most studies have considered meshes 1½ inches and larger. Rees (1957), in a study of seaward-migrating salmon, was one of the first to report in detail on the use of fine-thread experimental gill nets with meshes smaller than 1 inch. He used nets 60 feet long with 15- by 15-foot panels of ½-, ¾-, 1-, 1¼-, and 1½-inch mesh. Ricker (1937) and Eschmeyer and Bailey (1955) used gill nets with meshes 1 inch and smaller, but only briefly discussed catches in these small meshes. The use of nets 100 feet long with 25- by 6-foot panels of ¾-, 1-, 1¼-, and 1½-inch mesh is described in *The Progressive Fish-Culturist* (U. S. Bureau of Sport Fisheries and Wildlife, 1958).

MATERIALS AND METHODS

The small-meshed experimental gill nets used in 1957 were 75 and 90 feet long. The 75-foot nets had 15- by 15-foot panels of ½-, ¾-, ⅞-, 1-, and 1¼-inch mesh, and the 90-foot nets had 15- by 15-foot panels of ½-, ¾-, 1-, 1½-, 2-, and 3-inch mesh. Although these nets received some use in 1958, the nets used most that year were 50 feet long with 10- by 10-foot panels of ⅜-, ½-, ¾-, ⅞-, and 1-inch mesh. Nets of ¾-inch mesh 100 by 6 feet and 50 by 6 feet were also used during both years. Mesh sizes larger than 1 inch are not considered in this report because considerable data are available on the selectivity of these larger meshes.

Nets of all mesh sizes were made from 110-denier, 2-ply, white nylon except for one 10- by 12-foot panel of ⅜-inch-mesh, 70-denier, 2-ply, white nylon which was fished in 1958. Insufficient data were obtained for comparing thread sizes, and catches from all ⅜-inch-mesh nets were combined. For a discussion of thread sizes of nylon webbing, see Carrothers (1957). Setting and lifting fine-thread, small-meshed gill nets required extreme care. Nets were not lifted in rough water because they were easily damaged, and because excessive tension on the webbing decapitated small fish gilled in the nets. Vertical spacer lines were run from the float line to the lead line between each panel of webbing to reduce this tension.

Considerable damage to the nets occurred when large fish became entangled by their teeth or maxillae and tore the webbing as the nets were lifted from the water. The small meshes discouraged repair other than sewing together edges of large tears. Even with care, the nets usually lasted only one season.

Nets were fished from June 9 until October 6, 1957, and from May 21 until September 10, 1958. The nets were lifted every

[1] Gill-net mesh sizes in this paper are all stretched measure. References to bar or square-mesh measure found in the literature were converted to stretched measure by doubling.

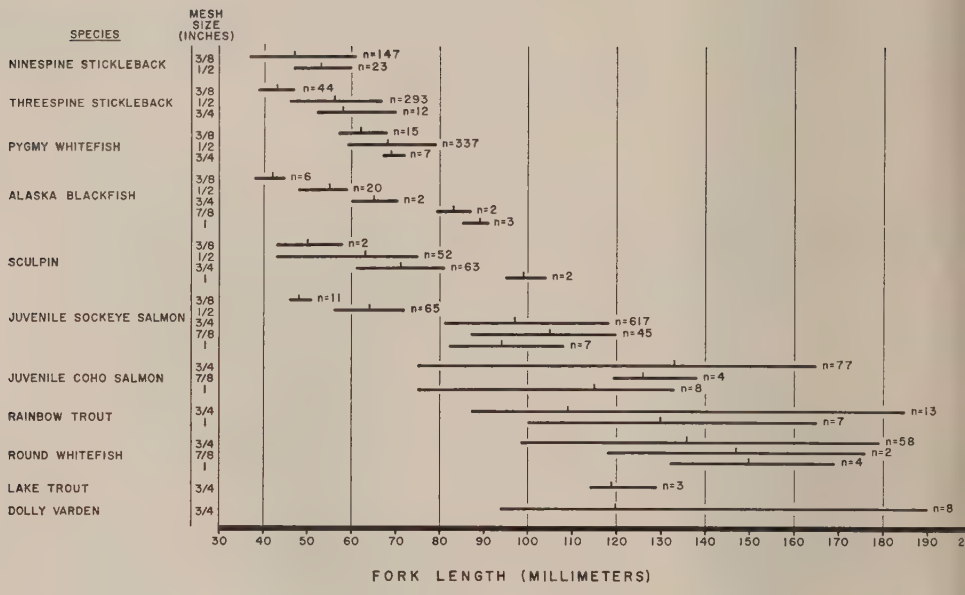

FIGURE 1.—Number, size range, and mean length of 12 species caught in small-meshed gill nets, Broo Lake, 1957–58. Horizontal bar shows range of fish lengths sampled by a particular mesh size; short verti bar shows mean fish length. One species caught by the nets (*Lampetra japonica*) is not shown because was represented by only three specimens, each from a different mesh size. Two species of sculpins (*Cott cognatus* and *C. aleuticus*) were not separated for purposes of this study.

24 hours unless the water was rough. Fishing sites were selected for depth, distance from shore, and type of bottom. Surface sets were fished over all depths; bottom sets were fished down to the 100-foot contour; and subsurface sets were suspended to a depth of 50 feet. The distribution of most fishes in Brooks Lake is closely associated with a peripheral zone of periphyton, algae, and vascular aquatic vegetation that extends into the lake to a depth of 50 feet. Most fishing effort was in this zone.

Catches of each species in a given mesh size were considered together, regardless of whether the thread sizes were different or whether the webbing was a panel in a graded series or a complete net of only one mesh size.

SMALL-MESH SELECTIVITY

Thirteen of the 20 species known to occur in Brooks Lake were gilled in the various sizes of small mesh. The smallest fish sampled was a 37-millimeter[2] ninespine stickleback (*Pungitius pungitius*). The smalle Alaska blackfish (*Dallia pectoralis*) sampl was 38 millimeters, and the smallest thre spine stickleback (*Gasterosteus aculeatu* was 39 millimeters. The smallest salmon sampled was a 46-millimeter sockeye salmo These are believed to be among the smalle fishes sampled with gill nets. Rees (195 caught 55-millimeter salmon in ½-inch-me nets, and the U. S. Bureau of Sport Fisheri and Wildlife (1958) reports catching an 8 millimeter trout in a ¾-inch-mesh net.

Juvenile sockeye salmon

Seven hundred and forty-five juvenile soc eye salmon from 46 to 120 millimeters lo were taken in all mesh sizes. Those caught ¾-inch mesh (617) ranged from 81 to 1 millimeters, and had a mean of 97.5 mil meters (Figure 1).

Juvenile sockeye salmon in Brooks La begin lake residence in April or May aft emerging from nursery gravels. During the first year of lake life they are called 0 juveniles. Those remaining in the lake 1 or

[2] Unless otherwise specified, all lengths are from tip of snout to fork of caudal fin.

ars are called 1+ or 2+ juveniles. The
m "smolt" refers only to juveniles migrat-
g seaward from the lake.

The range of mesh sizes used was probably
mpling the whole population of 1+ juve-
e sockeye salmon in the lake. All gill-net
tches of 2+ juvenile sockeye salmon in the
ke were made in June before the last of this
e group migrated from the lake. Because
tches in ¾-inch mesh (the median of the
e sizes used) were many times greater than
tches in the adjacent mesh sizes (Figure 1),
is likely that catches in ¾-inch mesh most
osely reflected the mean population struc-
re of 1+ juvenile sockeye salmon in the
ke during the two summers.

Fyke nets used in 1957 and 1958 to sample
036 1+ and 2+ smolts provided a less se-
tive gear for comparison with gill nets.
ie largest smolt sampled in the fyke nets
as 128 millimeters, and only four smolts
ken in fyke nets exceeded the maximum
ngth of juveniles sampled with gill nets.

In 1958, 0+ juvenile sockeye salmon,
hich were not sampled in 1957, were not
ught in gill nets in May or June. They
ere sampled with ⅜-inch mesh in early July,
th ½-inch mesh in late July, and with ¾-
ch mesh in August.

Recently attention has been given to the
lineation of specific mesh selection curves
Holt, 1957; Olsen, 1959; and McCombie
d Fry, 1960). The selection curve of a
esh size for a given species of fish may be
fined as the length–frequency distribution
at the mesh size is capable of sampling.

The 617 juvenile sockeye salmon caught in
-inch mesh do not represent the true selec-
on capabilities of the mesh on this species.
s noted by Peterson (1954), Holt (1957),
d others, the range of length frequencies in
population may exceed the selection curve
a given mesh. Conversely, when a popula-
on has a narrow spread in length frequen-
es, the selection curve may exceed the avail-
le population. This appears to be the case
ith catches of 1+ and 2+ juvenile sockeye
lmon in Brooks Lake.

The smallest juvenile sockeye salmon sam-
ed in ¾-inch mesh was 81 millimeters,
hich approaches the minimum selection ca-
abilities of the mesh for this species. In the smaller adjacent ½-inch mesh, the largest juvenile sockeye salmon caught was a 72-millimeter, 0+ fish. The 0+ juvenile sockeye salmon caught in ¾-inch mesh were 84 and 87 millimeters. This age group was present throughout both summers in a smaller size range, but was not sampled in ¾-inch mesh. The smallest salmonid sampled in ¾-inch mesh (Figure 1) was a 75-millimeter juvenile coho salmon (*Oncorhynchus kisutch*). Depending on the condition of the fish, the minimum selection limits of ¾-inch mesh on sockeye and young salmonids in general is probably between 70 and 80 millimeters.

The largest juvenile sockeye salmon sampled in ¾-inch mesh was 118 millimeters. The same mesh sampled young coho salmon, rainbow trout (*Salmo gairdneri*), and Dolly Varden (*Salvelinus malma*) as large as 165, 185, and 190 millimeters (Figure 1). Only two juvenile sockeye salmon sampled in ⅞-inch mesh were larger than those sampled in ¾-inch mesh. This also indicates that few of the larger juvenile sockeye salmon were present. The ¾-inch gill nets undoubtedly could have sampled larger juvenile sockeye salmon had they been available. Therefore, the true selection curve of this mesh includes a greater maximum size range and mean than were available in the Brooks Lake population.

Distributions of juvenile sockeye salmon caught in ⅜-, ½-, and ¾-inch mesh (Figure 1) showed that the size range of fish sampled increased with each increase in mesh size. An increased spread of selection curves with increases in mesh sizes may occur in larger meshes (McCombie and Fry, 1960). How closely the maximum lengths sampled in ⅜-inch and ½-inch meshes depict selection curve values is not known. The minimum lengths sampled are close to absolute selection values because the ⅜- and ½-inch meshes were fished throughout the period when 0+ sockeye salmon were too small for capture in these meshes.

Other species

When sample sizes were sufficient, selection curves for threespine and ninespine sticklebacks and pygmy whitefish (*Prosopium coulteri*) were similar to the normal distribution (Figure 2). Characteristics of the length

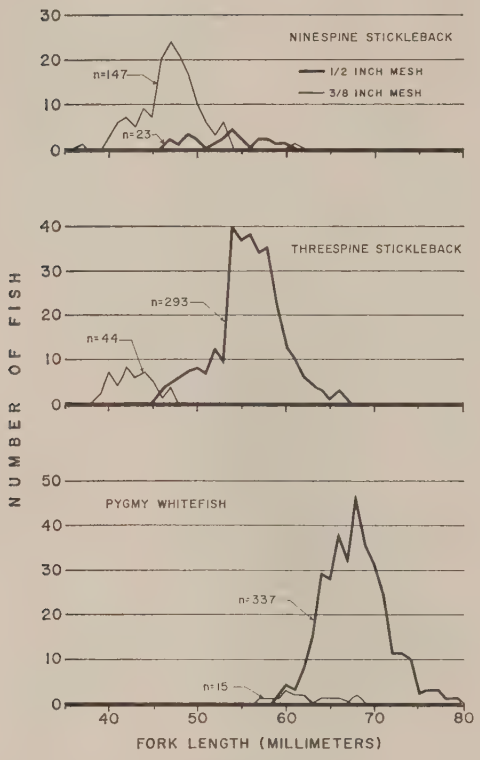

FIGURE 2.—Length–frequency distributions of sticklebacks and pygmy whitefish sampled in ⅜- and ½-inch-mesh nets, Brooks Lake, 1957–58.

distribution of sticklebacks and pygmy whitefish in Brooks Lake are not known; therefore, the accuracy with which ⅜- and ½-inch-mesh nets sampled these fishes is not known.

Either anatomical differences in the two sticklebacks, size differences, if they existed, or both accounted for the greatest number of ninespine sticklebacks being caught in ⅜-inch mesh, while most threespine sticklebacks were caught in ½-inch mesh. The role of anatomical form in mesh selectivity is shown in catches of threespine sticklebacks and pygmy whitefish in ½-inch mesh (Figure 2). The terete-shaped whitefish averaged longer in catches in ½-inch mesh than the sticklebacks, which are ovate in cross section and have pronounced dorsal and pelvic spines. Availability of different sizes in the two populations would also affect sample lengths.

Alaska blackfish and sculpins were the only fishes that increased in mean sample

TABLE 1.—*Number, range, and average fork len (inches) of fish in nongilled catches*

Species	Mesh size (inches, stretched meas			
	½	¾	⅞	1
Rainbow trout				
Number	1	24		2
Range	–	8.1–20.4		10.5–
Average length	20.9	13		15.
Round whitefish				
Number		9	1	
Range		8.5–14.4	–	
Average length		11.9	9.7	
Dolly Varden				
Number	2	1		
Range	15.9–18.7	–		
Average length	17.3	19.5		
Lake trout (*Salvelinus namaycush*)				
Number	2	16		2
Range	17.9–21.2	15.4–22.6		19.9–
Average length	19.6	20.0		20.
Arctic char (*Salvelinus alpinus*)				
Number				1
Range				–
Average length				16.
Adult sockeye salmon[1]				
Number		14		
Range		15.3–25.1[2]		
Average length		18.2		

[1] One hundred seventy-seven adults were caught in five mesh sizes. All live adults were released.
[2] Adult salmon lengths are mideye to fork of caudal

length in each of the five mesh sizes (Fig 1), although only one sculpin (75 millimeters) was sampled in ⅞-inch mesh. Round whitefish (*Prosopium cylindraceum*), rainbow trout, and Dolly Varden also increase in average size in catches in successively smaller meshes, but they were not sampled in smaller meshes. Juvenile coho salmon decreased in average length in three progressive mesh sizes. In this case small sample sizes and inadequate spread in length-frequency of available fish prevented normal expression of mesh selectivity.

Foul catches

Occasionally nongilled catches of large fishes were made in small-meshed nets (Table 1). These fishes were entangled either by their teeth or maxillae, and were not included as a part of the regular catch of gilled fish. Although Holt (1957) attributed bimodal and trimodal selectivity curves of larger mesh sizes to nongilled catches, our catches show little relationship to net selectivity. Random entanglement is suggested instead.

EFFICIENCY OF SMALL-MESHED NETS

To equate catches from the various panel dimensions, 75 square feet of webbing of a given mesh size fished for 24 hours was d

BLE 2.—*Average catches in 1958 that were 0.1 fish or greater per unit of fishing effort*[1]

Species	Mesh size (inches, stretched measure)		
	⅜	½	¾
venile sockeye salmon	–	–	0.1
gmy whitefish	–	0.9	–
reespine stickleback	0.1	0.7	–
nespine stickleback	0.7	–	–

[1] One unit equals 75 square feet of webbing fished for hours.

nated as one unit of fishing effort. The shing intensities of the various mesh sizes nged from 429 to 3,366 units of fishing fort for ⅜- and ¾-inch mesh. Juvenile ckeye salmon were caught in ¾-inch mesh a rate of 0.2 fish per unit of effort in 1957, d at a rate of 0.1 in 1958. Gill-net catches juvenile sockeye salmon in Brooks Lake ry considerably, depending on location and ason (Merrell[3]). Catches of other fishes d with other mesh sizes in 1957 were all low 0.1 fish per unit of effort. Average tches in 1958 that were 0.1 fish per unit effort or greater are shown in Table 2.

Individual catches of pygmy whitefish and icklebacks were as high as 40 fish per unit effort. The same net in the same location other times would fish for several days thout catching a fish. Because of the many riable factors affecting gill-net catches Moyle, 1950), and because of the varied nditions under which nets were fished, the ficiencies of catches during this study are orly understood.

Rawson (1951) selected 1½-inch mesh for e smallest panel in his sampling nets and ated that meshes smaller than 1½ inches ere relatively ineffective, even if the nets ere made of very fine thread. This ineffec- veness is apparent when mesh sizes 1 inch d smaller are compared with mesh sizes ½ to 5½ inches) more commonly used in perimental gill nets. Although the smaller eshes do provide a useful tool because they n sample smaller fishes, their value in uantitative assessment of fish populations is uestionable.

[3] Merrell, Theodore R. (1958) Field Operation eport, 1957, Red salmon studies, Brooks Lake. lmon Survival Investigations, Bureau of Commer- l Fisheries, Juneau, Alaska (processed). (Being vised for publication as U. S. Fish and Wildlife rvice Special Scientific Report: Fisheries.)

DISCUSSION

Catches in ⅜-, ½-, ¾-, ⅞-, and 1-inch-mesh gill nets indicate a sensitive selectivity among these small mesh sizes. Size ranges of the fishes available in some cases prevented full expression of this selectivity because specific mesh selection curves can exceed length frequencies available in the population.

The best estimates of 1+ and 2+ juvenile sockeye salmon length frequencies in the lake during 1957 and 1958 were from catches in ¾-inch mesh. Mesh sizes of ⅜ and ½ inch must be used to sample 0+ sockeye salmon smaller than 70 to 80 millimeters. Mesh sizes reported in this study could probably sample populations of juvenile sockeye salmon from 45 to 200 millimeters.

Sticklebacks, Alaska blackfish, and pygmy whitefish smaller than 40 millimeters can be sampled in ⅜-inch mesh. Different anatomical forms of these small fishes affect catches in various small meshes, indicating specific selection curves of each mesh for each species.

Gill-net meshes 1 inch and smaller have low catch efficiencies, but such mesh sizes provide effective gear where qualitative sampling of small fishes is desired.

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T. R. Merrell was in charge of the overall program at Brooks Lake. Dr. F. P. Meyer conducted the field work in 1957, while I did so in 1958. Dr. W. L. Hartman critically reviewed the manuscript and made helpful suggestions throughout the study.

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Collection and Analysis of Commercial Fishery Statistics in the Great Lakes

eat Lakes Fishery Commission

NICAL REPORT No. 5
mber, 1962

The Great Lakes Fishery Commission was established by the Convention on Great Lakes Fisheries, between Canada and the United States, ratified on October 11, 1955. It was organized in April, 1956 and assumed its duties as set forth in the Convention on July 1, 1956. The Commission has two major responsibilities: the first, to develop co-ordinated programs of research in the Great Lakes and, on the basis of the findings, recommend measures which will permit the maximum sustained productivity of stocks of fish of common concern; the second, to formulate and implement a program to eradicate or minimize sea lamprey populations in the Great Lakes. The Commission is also required to publish or authorize the publication of scientific or other information obtained in the performance of its duties.

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COLLECTION AND ANALYSIS OF COMMERCIAL FISHERY STATISTICS IN THE GREAT LAKES

by

RALPH HILE

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COLLECTION AND ANALYSIS OF COMMERCIAL FISHERY STATISTICS IN THE GREAT LAKES

by

Ralph Hile

ABSTRACT

Catch-effort statistics are submitted on closely similar monthly report forms by licensed commercial fishermen throughout U.S. and Canadian waters of the Great Lakes. This form was tested experimentally in State of Michigan waters in 1926; monthly submittal was required of Michigan fishermen beginning September 1927. Use of the form spread gradually to other states and Ontario; full coverage was achieved in 1950. The procedure for tabulation and analysis of the statistics also is the same in all states and Ontario.

Much of the present report is concerned with the development of the analytical procedure and the illustration, through example, of its operation. An early discovery was the need for completely independent tabulations of effort for each of the principal species. To meet this need, effort was charged to a species only on those days when some poundage was produced. At about the same time it was learned that the catch per lift of stationary gear, without any consideration of fishing time (nights out) before lifting, gives satisfactory estimates of fluctuations in abundance.

Later developments were concerned mostly with the use of catch-effort statistics for dissimilar gears to obtain single index figures for abundance and fishing intensity. The procedure now employed is described and illustrated.

Special circumstances have made necessary certain exceptions to the standard procedure. Exceptions made to date are listed and the reasons for them explained. Explanations are given also of certain special computational problems, and the disruptive effects of changes of regulation are reviewed.

INTRODUCTION

The extensive and diverse fisheries of the Great Lakes offer many unique situations. Despite their considerable area of 95,000 square miles, the lakes contain no international waters; the boundary between the United States and Canada is precisely defined. The 61,000 square miles that lie within the United States are subdivided—again by clearly defined boundaries—among the 8 bordering states. The states thus own the U.S. waters of

the Great Lakes and they have absolute jurisdiction over the fisheries within their several borders. All Canadian waters of the Great Lakes (34,000 square miles) lie in the Province of Ontario, but the fisheries are the property of the Canadian federal government. Under arrangements between the federal and provincial governments, however, Ontario has, in effect, power over its fisheries almost equal to that of any state.

The division of Great Lakes waters among 9 political jurisdictions has led to 9 largely independent approaches to management of the fisheries—regulations on licensing, boats, gear, size limits, closed season, ... The lack of uniformity is irritating to the industry and sometimes is economically burdensome. Many and sincere attempts have been made to ease the situation but improvements at best have been meager.

The collection and analysis of commercial fishery statistics stand in refreshing contrast to the confusing differences in regulation. All 8 states and Ontario collect these statistics by the same method and all statistical data are treated by the same analytical procedure. It is the purpose of this paper to review the origin and development of this statistical system, to explain the logic that underlies the analytical procedure, and to comment on various sources of weakness and strength.

The accounts of procedure given here are based almost entirely on work with the statistics for the State of Michigan waters of the Great Lakes. Usable records for other waters do not yet cover a sufficient span of years for the establishment of the base or reference period that is fundamental to the system of analysis.

Although this paper is concerned only with the collection and analysis of catch-effort data for major species, the tabulations include the recording of the take of all species. They supply then a full record of commercial production.

References to fishes throughout the paper are by common names. Most of these names conform with the approved list of the American Fisheries Society (1960) but a few are according to local or trade usage. To facilitate exact identification the following list of common and scientific names is offered; if the name used in this paper differs from the Society's approved common name, the latter is given in parentheses.

Common name	*Scientific name*
Blue pike	*Stizostedion vitreum glaucum*
Carp	*Cyprinus carpio*
Catfish (channel catfish)	*Ictalurus punctatus*

Chubs (deepwater ciscoes)	*Coregonus spp.*
Lake herring	*Coregonus artedii*
Lake trout	*Salvelinus namaycush*
Round whitefish	*Prosopium cylindraceum*
Sauger	*Stizostedion canadense*
Sheepshead (freshwater drum)	*Aplodinotus grunniens*
Smelt (American smelt)	*Osmerus mordax*
Sturgeon (lake sturgeon)	*Acipenser fulvescens*
Suckers	
Longnose	*Catostomus catostomus*
Redhorse	*Moxostoma spp.*
White	*Catostomus commersoni*
Walleye	*Stizostedion vitreum vitreum*
White bass	*Roccus chrysops*
Whitefish (lake whitefish)	*Coregonus clupeaformis*
Yellow perch	*Perca flavescens*

DEVELOPMENT OF THE REPORTING SYSTEM

The first move toward the development of the present statistical system in the Great Lakes was initiated by Dr. John Van Oosten in 1926. He was motivated by the knowledge that effective research and management of the Great Lakes fisheries required sound statistics on both the catch and the fishing effort expended to produce that catch; and further by the realization that the fisheries were so constituted that statistical data could not be collected effectively by agents at ports of landing.

The Great Lakes fisheries, unlike many marine fisheries, do not have a few major ports at which the greater part of the total production is landed. Instead, Great Lakes fish are landed at scores—indeed hundreds—of ports scattered along the 9,600 miles of shoreline. If records of catch and effort are to be had, they must be maintained and supplied by the individual operators. To test the feasibility of this type of reporting, Van Oosten designed a monthly report form that carried space for daily records of gear and catch and, with the assistance of the Michigan Department of Conservation, placed supplies with a group of cooperating fishermen.

The test of the new report was so successful that in September 1927 the State of Michigan made its regular submittal a requirement for all holders of commercial fishing licenses. The data on the early reports were incomplete and inaccurate in many respects, but the quality of the returns improved rapidly. By 1929 the statistics were sufficiently sound that analyses

could be started. These analyses of State of Michigan statistics have always been carried out in the Biological Laboratory of the Bureau of Commercial Fisheries in Ann Arbor, Michigan.

The inability of the Ann Arbor Biological Laboratory to handle additional reports and of states to undertake the work themselves hampered the extension of the reporting system to other Great Lakes waters. Of the few states that installed the system in the 1930's some later abandoned it because tabulation and treatment of the data could not be made. The use of monthly commercial fishing reports did, however, spread gradually. The years in which continuing submittals were started in the 8 states and Ontario were: Michigan 1927; Ohio 1931; Wisconsin 1936; Ontario 1946; Minnesota 1947; Illinois, Indiana, New York, and Pennsylvania 1950. The completion of coverage in 1950 followed an expansion of the Bureau program which made it possible to assure the newly cooperating states of adequate treatment of records.

The monthly report forms of the states and Ontario are closely similar and much the same as the one originally designed by Van Oosten. Principal differences among current forms are occasioned by differences in species produced and kinds of gear authorized. The major deletion from the original report has been a column calling for the nights out—that is, the number of days stationary gear was fished before it was lifted.

The head of each report form carries space for general information needed to identify and classify the report, including lake (if the state or province borders on more than one); name or number of boat; port of landing; commercial fishing license number; and name and address of licensee. The body of the report provides a line for day of the month for a record of: exact locality of fishing; kind and amount of gear; pounds of each species taken. A bottom line has space for the monthly total catch of each species, but the fisherman is not asked to make the addition. Reports of Ontario, Pennsylvania, Michigan, Illinois, and Minnesota carry a second bottom line for a record of the average monthly price received for each species, but submittal of price information is mandatory only in Ontario and Pennsylvania.

DEVELOPMENT OF ANALYTICAL PROCEDURES

The basic procedures for the treatment of the catch and effort statistics on the commercial fisheries of the Great Lakes were developed during the 1930's and were not in their final

form until the latter part of the decade. The rate of progress can be attributed to the peculiarly complex conditions in the Great Lakes fisheries that made caution and deliberation necessary. It was desirable further to see how the procedures performed over a period of several years. Caution was learned also from the publication of the premature paper on statistical methods by Hile and Duden (1933). One of the two major theses laid down—that concerning the overriding importance of fishing time in the estimation of fishing intensity and abundance from records for stationary gear—was shortly thereafter found to be erroneous.

The subsections that follow are rather closely in the order in which points had to be considered as the statistical program was developed. A general treatment of procedural problems, including exceptions to procedure and the basis for them, is reserved for later sections.

STATISTICAL DISTRICTS

The establishment of the boundaries of statistical districts was based principally on three criteria: a district must be large enough that the catch-effort data for the major species can be based on a substantial annual production; a district should not include a wide diversity of ecological situations; boundaries should be so placed as to minimize the number of reports that carry records of fishing in more than one district. Rarely could all of the three criteria be met satisfactorily by a proposed boundary and sometimes they conflicted sharply. The placement of almost every boundary, therefore, represented a compromise that was judged to be the best possible (Figs. 1-5).

The State of Michigan waters of the Great Lakes originally were divided into the following numbers of districts: Lake Erie 1; Lake Huron 6; Lake Michigan 11; Lake Superior 7. No occasion has since arisen to sub-divide the Lake Erie district or to change the boundaries of the Lake Huron districts. The number in Lake Superior soon was reduced from 7 to 6 by the combination of two districts, neither of which alone had sufficient production to provide sound records. The combined districts form the present district MS-2. Greatest difficulty arose in Lake Michigan where several district boundaries proved to be highly unsatisfactory. A broad reorganization of the northern area reduced the number of districts from 11 to 8. Five, however, of the 11 original districts (the present districts MM-1, 4, 6, 7, and 8) still have their original boundaries.

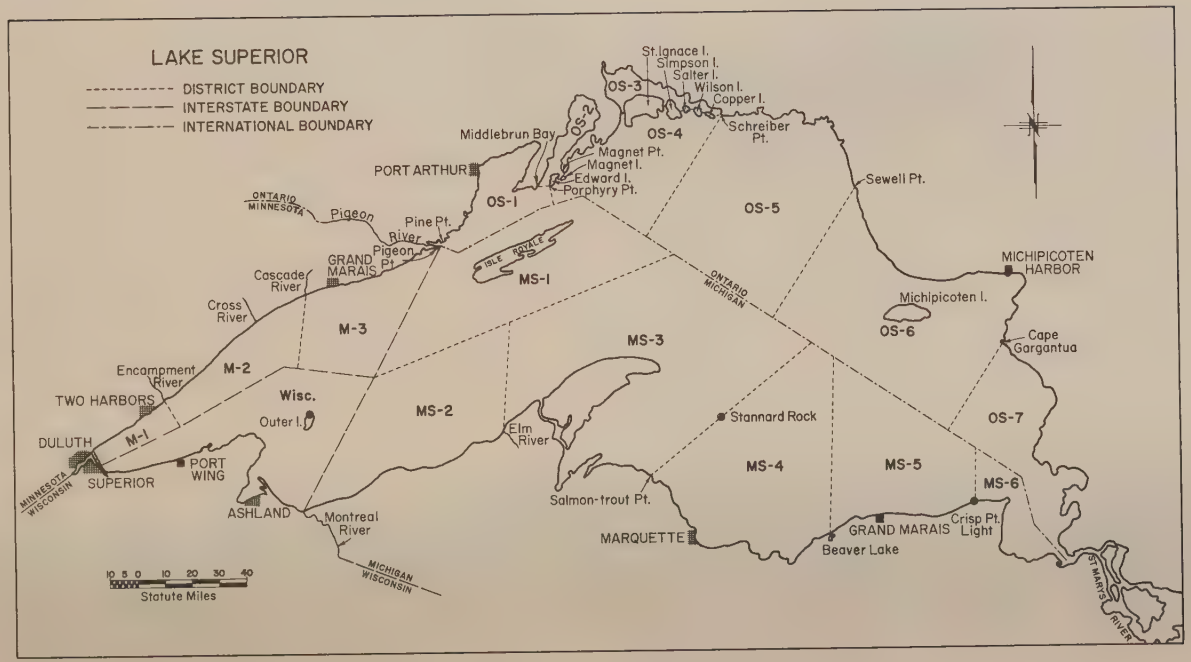

Figure 1.—Statistical districts of Lake Superior.

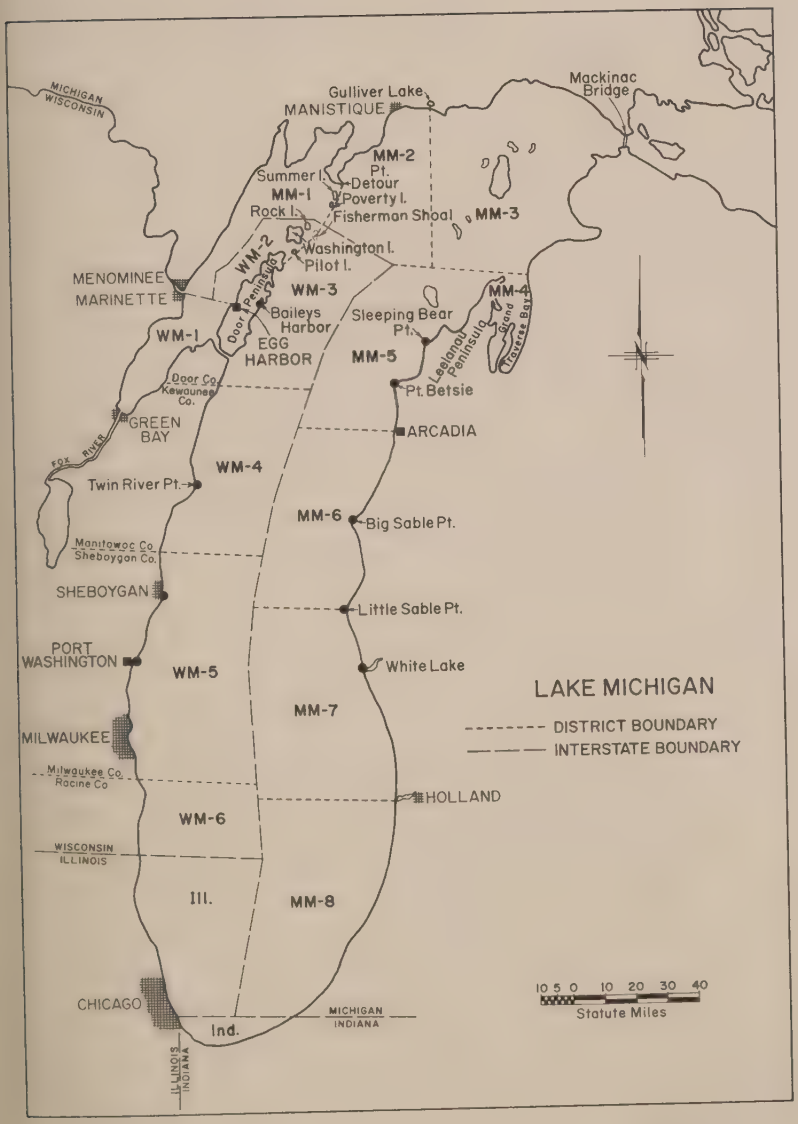

Figure 2.—Statistical districts of Lake Michigan.

Figure 3.—Statistical districts of Lake Huron.

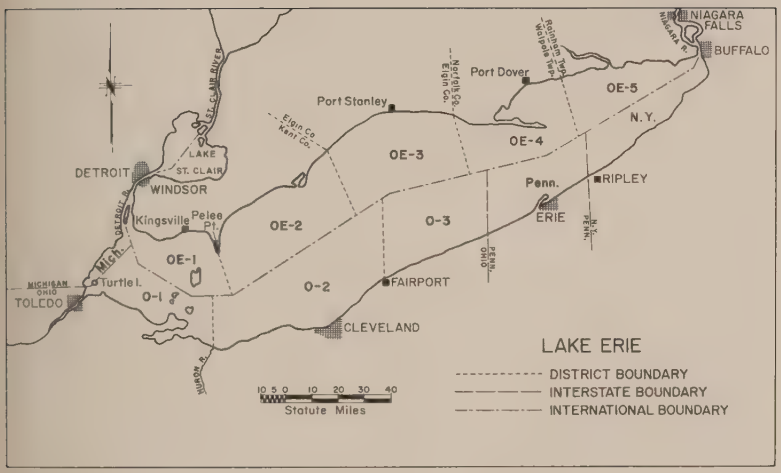

Figure 4.—Statistical districts of Lake Erie.

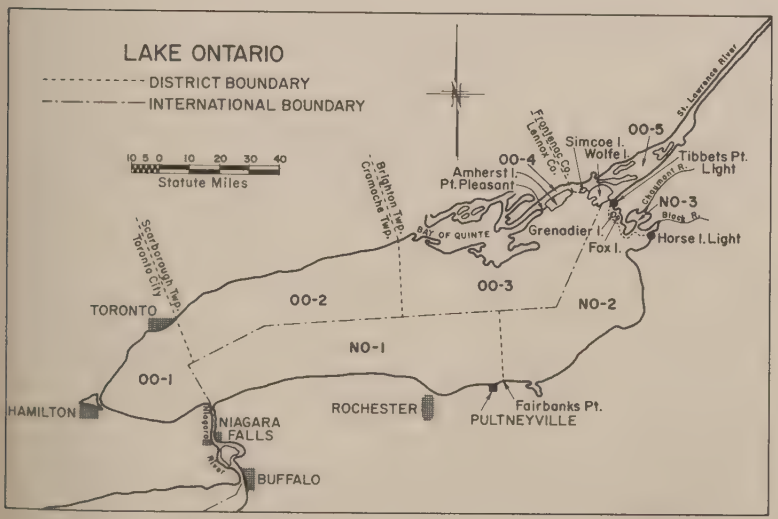

Figure 5.—Statistical districts of Lake Ontario.

The necessary reorganization of the original districts of northern Lake Michigan drove home an important principle. If a danger of "over-districting" exists, care should be taken to place boundaries so that consolidation can be achieved by the combination of pre-existing districts. The work involved in combination is limited and simple. The shifting of a district boundary to a new position, on the contrary, necessitates the retabulation of records for the districts affected.

A detailed review and criticism of the present districting of Great Lakes waters (described and charted by Smith, Buettner, and Hile, 1961[1]) could serve little purpose here. In the main, the present district boundaries appear to be satisfactory. Conceivably a combination of districts in Minnesota may be needed to give greater bulk of data and the open-lake districts of the New York waters of Lake Ontario still contribute scanty production even though they represent consolidations of former districts.

In a few situations, the conditions that dictated the original placement of boundaries no longer exist. The adjacent open-lake waters were included in the Saginaw Bay district of Lake Huron (MH-4), for example, to separate the whitefish grounds off the mouth of the Bay from the more northerly grounds of the Oscoda area and the southerly grounds of the Harbor Beach region. Now that whitefish production has fallen to a low level, the inclusion of the open-lake waters in district MH-4 is almost a handicap. If we were districting the lake now for the first time, MH-4 most likely would be restricted to Saginaw Bay proper and the offshore waters (which now produce principally chubs) divided between MH-3 and MH-5 or retained (with some small difference of boundaries) as a separate district. Should whitefish production again reach high levels, however, the present definition of MH-4 once more would become useful. It seems to be impossible to establish districts that will meet all needs in perpetuity. Neither is it practical to undertake a series of boundary shifts as conditions change. The recompilation of records that may cover more than 30 years entails far too much

[1] Figures 1-5 of the present paper are (with some slight modifications) from this publication. One of the changes has been a correction of a district boundary on the map for Lake Michigan. The boundary between MM-2 and MM-3 is not as stated and charted in the Smith, Buettner, and Hile report. It is instead a north-south line from the mouth of the Gulliver Lake outlet to the northern boundary of MM-5. The error arose partly from the lack of a precise definition of the Michigan-Wisconsin boundary when the districts were originally set up.

work and cost. It appears best to retain established districts except for combinations where they seem to be desirable. If an urgent need arises for information on an area that constitutes only part of a district, it is best to make special compilations from original records.

FISHING EFFORT

Units of effort

At the start of the tabulations, units of effort were set up for each of the major types of gear: gill nets; impounding nets; set hooks; and haul seines. A definition for trawls has been added recently. Definitions and comments are offered in the following paragraphs.

Gill nets: The lift of 1,000 linear feet of gill netting. Records are maintained separately for five ranges of mesh size, extension measure: bait (small chubs as bait for set hooks) or smelt nets, usually 1 1/2-1 5/8 inches; small-mesh nets, 2 1/8-3 inches but mostly near 2 1/2 and fished for such species as blue pike, chubs, lake herring, round whitefish, and yellow perch; large-mesh gill nets, mostly near 4 1/2 inches but as much as 6 1/2 inches, and fished mainly for lake trout, suckers, walleye, and whitefish; carp gill nets, usually 7-8 inches; sturgeon gill nets, usually 10-12 inches.

Impounding nets (pound nets, deep trap nets, shallow trap nets, and fyke nets): The lift of one net. The broad term "fyke net" includes such gear as hoop nets, the drop net of Green Bay, and the gobbler net. The gobbler has about the same fishing power as a fyke net, but the pot is supported by rectangular frames instead of hoops. The impounding nets are not classified by mesh size but the separation of trap nets into deep and shallow gives a large measure of separation for that gear. Deep trap nets, now fished only in the Michigan waters of Lake Huron, have meshes not less than 4 1/2 inches in the pot; the depth of the pot normally is from 25 to 40 feet but may be greater. The mesh size in the pot of shallow trap nets usually is under 3 inches, but may be 4 1/2 inches in Lake Superior where numbers are fished for whitefish; the depth of the pot ranges from 15 feet down to as little as 3 or 4 feet according to the principal species sought.

Set hooks: The lift of 1,000 hooks. The original tabulations are rounded to the nearest 0.1 unit (to the nearest 100 hooks). Set hooks include the floated hooks as well as bottom hooks fished for lake trout in Lake Superior and the bottom lines

formerly set for the same species in Lakes Huron and Michigan. They are fished also for catfish and rarely for other species.

Haul seines: One haul of a 100-rod seine. (Most, though not all seiners use the rod—16 1/2 feet—as a unit of length). The original tabulations are rounded to the nearest 0.1 unit (to the nearest 10 "rod-hauls").

Trawls: One hour of actual dragging.

In addition to the listing of "fishing effort" in terms of the units just defined the early tabulations (through 1934) carried a record of "fishing intensity" for the stationary gears—gill nets, impounding nets, and set hooks. The effort for a day was defined as the amount of gear lifted on that day. The intensity was the amount of gear lifted, multiplied by the number of days (nights out) the nets or hooks had fished before lifting. It was held that the fishing pressure of stationary gear is directly proportional to the length of time the net is in the water. The logic of this assumption was laid down by Hile and Duden (1933). Experience caused the validity of the assumption to be suspected early but the tabulation of fishing intensity was continued through a 6-year period. This tabulation provided material most useful in a study of the actual relation between fishing time and catch per lift—a point that is discussed later.

Effective fishing effort

The original or "test-run" tabulations of the statistics contained the following entries for each monthly report: total fishing effort; total fishing intensity; total catch in pounds of each species. When the annual totals of these entries were made and the catch per unit effort (or intensity) computed for each gear, it became obvious immediately that the system was falling short of its purpose of providing a measurement of the quality of fishing. The take of yellow perch, for example, might be less than 5 pounds per 1,000 feet of small-mesh gill net, though one with even casual acquaintance with the fishery knew that the true figure rarely fell under 20 pounds (else the fisherman suspended operations) and commonly was much greater. Again, the average take of whitefish per pound-net lift might be 10-20 pounds when the lifts actually ran from 50 to 100 pounds or more.

Examination of a series of reports made the cause of the difficulty clear. The total lift of small-mesh gill nets, for example, included not only nets that were set on yellow perch grounds and took perch but also those set in deep water for chubs or on spawning grounds for lake herring. These nets fished for chubs and herring rarely take any perch at all. Inclusion of them in the computation of the catch per unit effort

for yellow perch yielded a meaningless statistic. Similarly with pound nets—the large-mesh nets set for whitefish rarely take lake herring and whitefish seldom enter the small-mesh pound nets fished inshore for herring.

The examples of the preceding paragraphs illustrate a point but are oversimplified. In much of the Great Lakes fishing, especially in shallow water, several species are taken in good quantities in the same net. The problem, then, is not one of deciding for which single species the fisherman fished his gear. Rather it is one of obtaining a useful statistic on fishing effort for each species in a lift that produces several.

The distribution of a day's fishing effort among the species according to their contribution to the total catch was abandoned with little consideration. To illustrate the procedure, if 10 trap nets are lifted and yellow perch make up 38 percent of the catch, the species is charged with 3.8 trap-net lifts. If, on the next lifting day perch make up 27 percent of the total, they are charged with 2.7 lifts. Yet, the catch of perch may be identical on the 2 days; the change of percentage can result from change in the catch of other species. The assignment of effort thus has limited value.

It was decided next that either all or none of the day's fishing effort should be charged to each species for which records of effort are kept. and a basis was sought for the decision. The requirement that the species contribute at least a minimal percentage of the take could not be used since that percentage must vary according to the catch of other species. The basis for decision had to be founded wholly on the records for the species under consideration. It needed to include also the requirement for some minimal catch of the species in order to exclude fishing conducted where the species does not occur. The establishment of some small but significant minimum level of catch per unit effort was considered but abandoned because of the difficulty of setting truly realistic values for each species and gear in each district; furthermore, fishing effort chargeable in years of high abundance might be rejected in years of low abundance. The only practical requirement for a minimum take proved to be any catch at all. Thus all the gear lifted by a fisherman on a particular day is charged to a species taken, even if the amount is as little as a pound.

It is not held that effective fishing effort as defined and used provides a wholly unbiased measure of fishing pressure. It has been employed because a better one could not be devised for a fishery in which most nets are set with the intent and expectation of taking several species simultaneously. Effective

fishing effort does not provide for "water hauls" but in the Great Lakes this provision would serve small purpose; the distribution of fish varies little, other than seasonally, from year to year and is such that nets fished on grounds occupied by a species almost invariably take some quantity of that species. Indeed, the lack of provision for water hauls is probably overcompensated by the charging of the entire amount of gear lifted against a species on days when the actual catch is extremely small.

Other possible sources of bias exist but discussion of them here would be little to the point since no measure of their importance can be given and no remedy can be offered.

It has been comforting to learn from the many years of record (now exceeding 30 in State of Michigan waters) that the catch per unit of gear computed from effective fishing effort does reflect clearly known changes in the quality of fishing. How finely these changes are measured is not known. The degree of accuracy no doubt varies with species, area, and local conditions of the fishery. If production is high and the fishery not disrupted by changes of regulation, gear, or fishing method, the sensitivity of catch per unit of effort may be high.

The effective fishing effort is not a distributive statistic. It provides a separate and independent accounting of fishing effort for each species. To illustrate the point, let it be assumed that a fisherman lifts 10 shallow trap nets on each of 15 days within a month and that he lands yellow perch every day, walleyes on 10 days, suckers on 7 days, . . . The assignments of fishing effort then become: yellow perch 150 net-lifts (identical with the total fishing effort); walleyes 100 net-lifts; suckers 70 net-lifts; . . . .

The adoption of effective fishing effort as a measure of fishing pressure calls immediately for a selection of species for which the record will be maintained. It would be unduly costly to tabulate effort for the numerous minor species that are caught in relatively small quantities. The species that are classed as "major" or "principal" vary according to species composition in different waters but decisions for the State of Michigan provide an example. The principal species for which records are kept in every district except the Erie district are: lake trout, whitefish, lake herring, chubs (all species collectively), walleye, yellow perch, and suckers (white suckers and redhorse suckers combined; longnose suckers excluded). The original list included also sauger and carp for the Saginaw Bay district (MH-4); the catfish was added in this district later and data from reports for early years tabulated to give a full record. When smelt became plentiful, the species was classed as princi-

pal in the Green Bay district (MM-1) and northeastern Lake Michigan (MM-3). The Lake Erie district was assigned no "principal" species because of the belief that conditions in the area were so nearly uniform as to justify a mere tabulation of the total fishing effort and the catch of each species (the method of tabulation in the "test-run"). Experience proved the belief to be erroneous. For a number of years effective fishing effort has been tabulated for the following species in the Michigan waters of Lake Erie: carp, catfish, sheepshead, suckers (no longnose suckers in the district), walleye, white bass, and yellow perch. The Lake Erie statistics for a good span of the earlier years remain, however, to be retabulated.

The establishment of principal species (or groups of species) for which effective fishing effort is tabulated in all State of Michigan districts of the three upper lakes does not mean that each species or group is taken in sufficient quantity in each district to yield reliable data. Rather, it was held that the uniform tabulation procedure was more economical and more likely to be accurate than one with numerous exceptions. This view was especially justified in the earlier years when much of the tabulation had to be done by hand (data are now handled by IBM equipment) by staff of limited experience. Actually, adherence to the procedure entails relatively little additional work.

Elimination of the time factor

The tabulation of catch-effort statistics on the commercial fisheries of the Great Lakes had not been underway long before examinations of the fishing reports gave rise to strong skepticism as to the validity of the assumption that the fishing intensity represented by the lift of stationary gear is proportional to the length of time (nights out) the gear fished before it was lifted. True, nets that had been out the greater length of time usually had the larger catches but the improvements of catch with increase of time were small. Because sound knowledge of the true relation of fishing time to catch was fundamental to the development of proper analytical procedure, a detailed inquiry into the matter was undertaken. This study covered every important stationary gear fished in the Great Lakes, including the two principal mesh sizes of gill nets. The relation between nights out and catch was examined not only for the total catch but also for individual species in the same gear.

The detailed results of the study of the relation between fishing time and catch were not published but rather placed in a manuscript report (written by Hile) for the statistical files. Certain of the data were published, however, by Hile (1935),

Van Oosten (1935), and Van Oosten, Hile, and Jobes (1946).[2] Principal findings and conclusions in the time-catch investigation were:

1. The catch improved with increase of fishing time but the increase was far less than proportional. The catch of gear out 2 nights, for example, averaged less than 20 percent above the take in gear out 1 night. The trends were similar for all stationary gears and for the individual species.
2. The most precise catch per unit effort for judging the availability (abundance) of fish is neither the catch per lift nor the catch per night, but rather the catch per lift adjusted for fishing time from an empirically determined curve of the regression of catch on time.
3. The mean annual fishing time for a particular gear in a single district varied within narrow limits.
4. Because of the limited mean annual variation in fishing time, estimates of annual fluctuations in abundance based on catch per lift and on catch per lift, adjusted for fishing time, differed insignificantly. The cross multiplication of amount of gear lifted and number of nights out is therefore, not necessary.

The discovery that the amount of gear lifted without regard to time was a satisfactory measure of fishing effort eliminated the most costly, tedious, and time-consuming step in the tabulation of catch-effort statistics. The "fishing intensity" was eliminated from the original tabulations. The same term is now employed in an entirely different sense as is explained in the next subsection.

INDICES OF ABUNDANCE AND FISHING INTENSITY

The major problem was the development of single descriptive index figures for abundance and fishing intensity from records of catch per unit effort (CPE) and effort (E) for such dissimilar gears as gill nets, pound nets, set hooks, ... If almost the entire catch of a species is produced by a single gear (nearly all chubs for example, were caught by small-mesh gill nets before the recent start of trawling) the fluctuations of abundance can be described readily by expressing the CPE for each year as a percentage of the unweighted mean of the annual

[2] Those interested in this subject should consult also the article by Kennedy (1951) on the relation of nights out and catch per net in the gill-net fishery of Great Slave Lake.

values for a base period of reference. The records of the annual amount of gear lifted provide the basis for a similar series of intensity indices (a small adjustment of the figures may be needed, as is explained later in this subsection, to account for the portion of the catch not taken by the principal gear). A one-gear fishery, however, is exceptional in the Great Lakes; consequently, a more general method of analysis had to be devised.

The procedure that was developed requires first a record of the unweighted base-period mean of the annual CPE for each gear that was important in the production of a species in a district. (This "base" or "reference" period in State of Michigan waters is 1929-43.) Once these averages are in hand the abundance and fishing intensity for a particular year are computed as follows:

1. The production that would have been made had the CPE been exactly at the 15-year mean is determined from the current-year values of E for each gear included in the estimation of abundance. These figures are expected catches (Ex).
2. The expected catches, determined separately for each gear, are added to obtain the total expected catch.
3. The true catches of the same gears are totaled to obtain the actual catch (Act).
4. The ratio of the actual to the expected catch, expressed as a percentage, is the abundance index (Ab).
5. The fishing intensity (Int) is determined by adjusting the total expected catch upward to include the intensity represented by the take in gears not employed in the estimation of the abundance index. Fishing intensity is, therefore, computed originally in terms of pounds of fish. For publication, the intensity is expressed in one or both of two forms:

    a. A percentage index in which a value of 100 corresponds to the base-period average intensity in pounds for the species and district.
    b. A unit index (U) in which 100 units represent the base-period average intensity in pounds for the species in the combined districts of the lake and state. The sum of the units for the individual districts thus provides an index for the combined districts that is parallel to the percentage index which holds only within a single district.

The preceding brief outline of procedure can be understood best from an actual illustration, based on materials from the statistical files—the "cover sheet" and the 1954 data on the fishery for white and redhorse suckers in the Green Bay district of the State of Michigan waters of Lake Michigan (MM-1—designated merely as M-1 in the State of Michigan files). Both the cover sheet (table 1) and the 1954 sheet (table 2) are exact copies of the original handwritten records in the sense that all original abbreviations and symbols have been retained. Several of the abbreviations have already been explained. Those referring to fishing gears are:

2+ and 4+, small-mesh and large-mesh gill nets of mesh sizes as stipulated in the section on units of effort.

Pd, pound net

ST, shallow trap net

Fy or F&H, fyke or hoop nets

Table 1.—Copy of averages and factors employed in the estimation of abundance and fishing intensity for white and redhorse suckers in district MM-1

[See text for explanation of abbreviations]

M-1 Suckers
Averages, factors 1929-1943

	CPE
4+	24.16
Pd	63.19
ST	83.46
Fy	67.92

Int (U)	= Int	(#) x 811787	(U *ca.* 12,300#)
Int (%)	= Int	(#) x 134069	(100 *ca.* 746,000#)

The cover sheet carries all information required for the estimation of abundance and fishing intensity for white and redhorse suckers in this district (a similar sheet appears at the start of the folder for each "principal" species in each district). The first set of figures is the unweighted base-period (1929-43)

Table 2.—Copy of statistical data sheet for white and redhorse suckers, district MM-1, 1954

[See text for explanation of abbreviations and computational procedures]

STATE OF MICHIGAN LAKE MICHIGAN DISTRICT 1 1954	White and redhorse suckers				STATE OF MICHIGAN LAKE MICHIGAN DISTRICT 1 1954	
	2+	4+	Pd	ST	F & H	Σ
Jan.	1	4,494	23	5,086	530	10,134
Feb.	19	6.733	5	1,935	79	8,771
Mar.	4	10,640	4	3,766	1,751	16,165
Apr.	. . .	. . .	. . .	1,206	. . .	1,206
May	27	12	740	4,455	. . .	5,234
June	120	. . .	4,581	21,964	1,155	27,820
July	83	. . .	4,225	20,137	275	24,720
Aug.	102	. . .	33	26,516	197	26,848
Sept.	498	170	1,345	60,525	397	62,935
Oct.	398	706	1,683	28,331	428	31,546
Nov.	112	1,029	45	13,506	366	15,058
Dec.	44	11	. . .	970	. . .	1,025
Total	1,408	23,795	12,684	188,397	5,178	231,462
E	2+	4+	Pd	ST	F & H	
Jan.	1	367	14	81	8	
Feb.	16	527	4	198	8	
Mar.	6	656	2	249	18	
Apr.	. . .	. . .	. . .	40	. . .	
May	19	13	30	131	. . .	
June	59	. . .	136	676	10	
July	55	. . .	40	394	7	
Aug.	33	. . .	2	355	4	
Sept.	89	30	33	910	42	
Oct.	226	79	134	886	7	
Nov.	81	114	5	514	25	
Dec.	14	2	. . .	64	. . .	
Total	599	1,788	400	4,498	129	
CPE	. . .	13.31	31.71	41.88	40.14	
Ex	. . .	43,198	25,276	375,403	8,762	

Σ	Ex	452,639
Σ	Act	230,054
Ab		50.8
Int	#	455,634
	U	37.0
	%	61

mean CPE (pounds of fish)[3] for each gear employed in the estimation of abundance. The next item, Int (U), is a factor for converting fishing intensity in pounds into units that may, as has been stated, be added to give an index figure for the combined districts. This factor is the same for suckers in all State of Michigan districts of Lake Michigan. The second factor converts intensity in pounds to the percentage index that applies only to the district under immediate consideration. Both of these factors are reciprocals but without any indication of their true decimal value. To aid in the placement of the decimal, approximate values of the unit (fishing intensity of about 12,300 pounds) and of the 100-percent level (fishing intensity of roughly 746,000 pounds) are added at the right.

The first step in the treatment of the 1954 data (table 2) is the determination of the CPE in 1954 for each of the four major producing gears. The catch per unit of 1,000 linear feet of large-mesh gill nets lifted was, for example, 23,795/1,788 = 13.31 pounds. Figures for pound nets, shallow trap nets, and fyke and hoop nets are similarly computed. The CPE figures for 1954 are for the record; they do not enter directly into the estimation of the abundance index.

The second step is the determination of the poundage of white and redhorse suckers that would have been produced in 1954 had the fishing success for each gear been exactly at the average for the 15-year base period of 1929-43. Had large-mesh gill nets, for example, taken 24.16 pounds per 1,000 feet instead of the actual 13.31 they would have produced 1,788 x 24.16 = 43,198 pounds rather than the actual 23,795 pounds.

The sum of the expected catches in four gears in 1954 was 452,639 pounds. They actually took 230,054 pounds. The actual take expressed as a percentage of the expected gives the abundance index of 50.8.[4] Abundance indices computed by this procedure do not add to $100n$ within a base period of n years (Hile, 1937), and hence must be adjusted. If, for example, the mean abundance index for the reference period proves to be 103.7, each index in the series is multiplied by 1/1.037 = 0.96432 to adjust the values to a mean of 100. No adjustments are made for the years following the base period.

[3] For computational reasons, values of CPE are carried in file records to the second decimal. Published figures are rounded to the nearest pound.

[4] The abundance index is rounded to the nearest whole figure for publication.

The best estimate of fishing intensity in pounds is slightly greater than the total expected catch since an adjustment should be made to cover the 1,408 pounds taken in small-mesh gill nets, a gear that did not enter into the estimation of abundance. The adjustment is accomplished by dividing the ratio of the actual to the expected catch into the grand total catch for all gears: 231,462/0.508 = 455,634. The adjustment here is almost trifling, but often it is substantial. In other words, the fishing intensity for white and redhorse suckers in northern Green Bay in 1954 was at a level that would have yielded 455,634 pounds had fishing quality been exactly at the base-period "normal" for all gears.

The estimated fishing intensity in pounds represented 37.0 units. One unit is 1/1,500 of the total fishing intensity in pounds for all State of Michigan districts of Lake Michigan in 1929-43. Examples of the distribution of intensity units among districts and of their summation to provide lake-wide indices have been given for lake trout in Lake Huron by Hile (1949), Lake Michigan by Hile, Eschmeyer, and Lunger (1951a), and Lake Superior by Hile, Eschmeyer, and Lunger (1951b).

The 1954 fishing intensity in pounds for suckers in northern Green Bay amounted also to 61 percent of the 1929-43 mean for this district.

A peculiar feature of the system of computing fishing intensity in terms of the expected catch in pounds is the flexibility it gives to the basic units of effort. For example, three of the gears used in the estimation of abundance and fishing intensity for white and redhorse suckers in northern Green Bay (MM-1)—large-mesh gill nets, pound nets, and shallow trap nets—are employed also in northeastern Lake Michigan (MM-3). The 1929-43 mean CPE (pounds) in the latter district ran: gill nets 11.09; pound nets 23.64; shallow trap nets 145.36. Comparison of these figures with those of table 1 shows that the expected catches per unit effort (15-year mean CPE) for large-mesh gill nets and pound nets in MM-3 were less than half those in MM-1; the average CPE for shallow trap nets in MM-3, on the other hand, was almost 1 3/4 times that for MM-1. It is possible, therefore, for identical quantities of gear fished in different districts to contribute different numbers of intensity units to the total for a lake. Within a single district, fishing intensity varies directly with the effort (amount of gear fished). For combined districts, the variation is not according to the sum of the effort units for the different gears in the several districts, but rather reflects the total fishing intensity in pounds computed independently for each district.

In the combination of abundance indices to obtain estimates for groups of districts or all districts within a lake and state, the index for each district has been weighted by the percentage the district contributed to the total production in all districts over the base period.

EXCEPTIONS TO STANDARD PROCEDURE

In the development of analytical methods an attempt was made to arrive at a procedure that would have wide applicability. The attitude was held, nevertheless, that exceptions to procedure should be made when they contributed to the attainment of the true goal of obtaining the best possible information on the fluctuations of the fisheries for the principal species. Experience proved that certain exceptions were in fact needed. They were not numerous but a listing of those made or contemplated and justification for the decisions are desirable. Others may be made later; as a matter of procedure the statistics for a particular species are placed under closest scrutiny when the files are entered to obtain materials for a report on the fishery or for statistics in support of biological studies.

WEIGHTING OF ABUNDANCE INDICES

It has been necessary to make only one exception to the procedure of weighting the abundance index of each district by the percentage the district contributed to the base-period production of all districts to obtain estimates of abundance for combinations of districts. The development and expansion of the fishery with deep trap nets in Lake Huron so disrupted the typical distribution of the catch of whitefish among the districts that Van Oosten, Hile, and Jobes (1946) held it preferable to weight abundance indices according to the percentage of whitefish taken in each district in a single year, 1929. It is unlikely that a similar extreme situation will appear soon again.

MODIFIED DEFINITIONS OF DISTRICTS

These modifications have included: the pooling of data for different districts for particular species to gain greater bulk of statistical data; assignment of fishing to districts according to nature of catch rather than on the basis of the precisely defined

boundaries; ignoring of boundaries in favor of the arbitrary assignment by ports.

The pooling of districts has been limited to date to the southerly State of Michigan districts of Lake Michigan. Here the districts MM 6, 7, and 8 have been combined for studies of walleye (Hile, 1937) and lake herring (Hile and Buettner, 1955) and the records for yellow perch have been pooled for two pairs of districts (MM-5 and 6; MM-7 and 8). All of these combinations were justified by similarities of trends in the districts for which data were combined. Combinations are made after the data are tabulated and annual totals of catch and effort determined for the districts separately.

Smith, Buettner, and Hile (1961) defined the boundary between MM-1 and MM-2 precisely but the actual assignment of fishing has been on the basis of species caught rather than the defined boundary. The effective difference between the two methods would be small. The boundary of MM-1 was set originally to the east of the islands that separate northern Green Bay from Lake Michigan proper to include in the district the fishing for whitefish immediately outside the islands. Accordingly, any large-mesh gill nets that took whitefish and all deep trap nets (basically whitefish gear) fished along the east side of the islands have been assigned to MM-1. Large-mesh gill nets fished deep enough to take only lake trout have been assigned to MM-2, as have been also small-mesh gill nets fished for chubs.

The boundary between MM-2 and MM-3 has been ignored in the assignment of chubs caught along southeasterly courses out of Manistique. All have been placed in MM-2 even though the nets actually were set across the border in the western part of MM-3. This procedure separates the statistics for the chub fishery of the northern part of the open lake from the somewhat dissimilar fishery for chubs in the eastern part of MM-3, between the islands and the mainland. The boundary between the two districts holds, of course, for other fishing.

A similar procedure has been established at Rogers City, Lake Huron, which lies almost exactly on the boundary of MH-1 and MH-2. All chubs landed at Rogers City are assigned to MH-1, regardless of the actual location of the nets, to keep the records separate from those for the chub fishery out of Alpena in the southern part of MH-2. The boundary between MH-2 and MH-3, however, is observed strictly.

EXCEPTIONS TO EFFECTIVE EFFORT

A situation was found in Lake Superior that required exception to the principle that fishing effort shall be charged to a species provided any quantity of the species is taken. In several districts of the lake, small poundages of lake herring are produced in small-mesh gill nets set in deep water for chubs. Gangs of chub gill nets typically are long—often 20,000 to 25,000 feet—and the catch per unit of effort of lake herring in them rarely exceeds a small fraction of a pound. The gangs fished inshore for lake herring are short—a few thousand feet—and take herring at a high rate that normally averages several hundred pounds per 1,000 feet. The charging of chub gill nets that take lake herring to the fishing effort for lake herring would cause misleading distortion of the lake herring statistics. The effort of the chub nets is accordingly excluded from the lake herring statistics and the small catches of herring are entered in the records as produced by small-mesh gill nets without data on effort.

As was seen in the example of table 2, determinations of CPE and estimates of abundance have been based typically on annual totals of catch and effort. The first statistical review of a fishery (Hile, 1937) disclosed, however, a situation in the Saginaw Bay district (MH-4) that required deviation from this procedure. The production of walleyes in large-mesh gill nets fell into two entirely distinct phases: an intensive April fishery on the spawning run fairly deep in the bay that yielded the bulk of walleye production by the gear; small-scale production of walleyes in whitefish gill nets in other months in the outer bay or off the mouth. Quantities of gear per lift were small and the CPE ran high in April; the gangs of whitefish gill nets were long and the catches and CPE of walleye both were extremely small. Because the effort expended in the whitefish fishery varied widely from year to year the CPE for walleyes, computed from annual totals, also could fluctuate greatly even when the CPE in the main April fishery was stable. Calculations of CPE for walleyes in large-mesh gill nets accordingly were based exclusively on the April records. The exclusion of data for the other months corresponds in a sense with the exclusion of the fishing effort of Lake Superior chub gill nets that take small quantities of lake herring.

The experience with gill-net fishing for walleyes in Saginaw Bay inspired alertness for other situations in which the determination of CPE and abundance should not be based on annual totals of effort and catch. Indeed the next statistical

review of a major fishery (Van Oosten, Hile, and Jobes, 1946) was preceded by detailed comparisons of estimates of fluctuations as determined from annual totals of catch and effort for whitefish and from the statistics for the months in which the bulk of the catch was taken. The restriction of the statistics to the "major season" gave much higher annual figures for CPE but the annual fluctuations of the abundance index were nearly the same from the two sets of data. Annual catch and effort totals have been satisfactory for other published statistical reviews except smelt (Van Oosten, 1947; Hile, Lunger, and Buettner, 1953), where month-by-month records were needed to describe the fishery in northern Green Bay.

A statistical study, soon to be undertaken, of the lake herring in Lake Superior almost surely will require a separation of records for the November-December spawning-run fishery (which accounts usually for 85 percent or more of the total annual production) from those for the remainder of the year. Similar situations may be uncovered in still other fisheries as the file records are employed for statistical reviews.

SPECIAL COMPUTATIONAL PROBLEMS

ESTIMATES OF BASE-PERIOD CATCH PER UNIT EFFORT FROM INCOMPLETE DATA; ADJUSTMENT FOR CHANGED EFFICIENCY OF GEAR

The appearance of a new gear in a fishery, the disappearance (or decline of fishing effort to inconsequential levels) of an established gear before the end of the base or reference period, and the fluctuations in the fishing effort for an important gear so wide that reliable determinations of CPE can be made for only part of the years within the base period all offer the same problem—the estimation of a base-period CPE (such as those listed in table 1) when data on the gear are not available for all years within the period. The problem is similar when the fishing capacity of a gear suddenly is changed as occurred with shallow trap nets fished for walleyes in northern Green Bay (Hile, Lunger, and Buettner, 1953; Pycha, 1961). An increase of efficiency similar to the one that led Pycha to adjust the "normal" CPE for walleyes taken by shallow trap nets in MM-1, required a change in the "normal" CPE for lake herring in shallow trap nets in MH-4, but Hile and Buettner (1959), omitted reference to the adjustment as inappropriate in the brief discussion in their article.

The estimation of a base-period CPE from incomplete data

requires first the determination of the mean of the annual CPE for the gear with incomplete records and subsequently the adjustment of that mean according to the CPE (expressed as percentage indices) of other gears that produced the same species in the same district in the same years. The procedure can be understood best, perhaps, from an example (table 3). Let it be assumed that gear A has made its appearance in a district where gears B and C have been fished continuously and that it is wished to determine a "normal" CPE for gear A on the basis of 5 years of record (years 7-11 within the base period).

Table 3.—Illustration of procedure for estimation of a mean base-period CPE for gear fished through only part of the base period

[See text for explanation]

Year in base period	CPE (pounds)	CPE (percentage of base-period mean)	
	Gear A	Gear B	Gear C
7	37.91	105	110
8	49.32	129	141
9	44.24	120	110
10	38.17	98	95
11	41.79	108	102
Average	42.29	[1]111.8	

[1] Unweighted mean for 10 entries.

The mean CPE for gear A was 42.29 pounds. The unweighted mean for the CPE of gears B and C, each expressed in terms of percentages of the average CPE for the base period was 111.8. The CPE for gear A for the base period is estimated, therefore, as 42.29/1.118 = 37.83 pounds. The procedure is similar for estimating the adjusted base-period CPE for a gear in which the efficiency has changed. Once the new level of efficiency has been established the gear is merely treated as new.

If a newly introduced gear interferes with the fishing of existing gears and/or leads to a sharp drop or discontinuation of their use, estimates of the type just illustrated become undependable. Van Oosten, Hile, and Jobes (1946), for example, considered their estimates of the "normal" CPE for deep trap nets in MH-5 and MH-6 to be highly untrustworthy. They held that abundance indices for whitefish in these districts could be compared within the period before the deep trap net became

dominant and within the period after it had become the principal gear, but warned against comparisons between these two periods.

Adjustments of the base-period CPE of an existing gear to accommodate changes of efficiency also are subject to some error since the changeover normally comes about over a period of years, not suddenly (Pycha, 1961).

The disappearance of a gear used in the estimation of abundance offers no computational problems if it comes about later than the last year of the base period. The introduction of new gear calls for the estimation of a base-period CPE regardless of the time of occurrence.

The greatest recent change in the efficiency of gear—that resulting from the change from cotton to nylon twine in gill-nets—found the Laboratory staff in poor position to gain sound quantitative data on the actual increase of efficiency. Normally, staff members would obtain the data directly from fishermen during the period of changeover. Regrettably, however, pressures arose for legal restrictions on nylon and persisted through and beyond the period of change for most gill-net fisheries and it was not discreet to ask fishermen to give records, privately or on their official monthly reports, on such a highly controversial matter. Nor has the Bureau been in position to conduct the extensive experimental fishing to resolve the question for a variety of species in a number of areas. Our one study has been limited to experimental fishing with nylon and cotton gill nets for lake trout in a single area (Pycha, in press).[5]

Even if discriminating estimates of the relative efficiency of cotton and nylon gill nets could be obtained today, the application of our findings for the "correction" of earlier records would be of questionable dependability in fisheries in which the characteristics of the present stocks differ greatly from those of earlier years. The size distribution of lake trout stocks of Lake Superior and of whitefish of Lakes Huron and Michigan have been altered greatly. In the latter two lakes both the size and species composition of chub populations have changed. Furthermore, the change from cotton to nylon gill nets proceeded at different rates in different areas and fisheries. In fact, both kinds of gill nets still are fished in the lake herring fishery in parts of Lake Superior, and possibly in other fisheries in various lakes. Still another complicating factor lies in the changes that

[5] "The relative efficiency of nylon and cotton gill nets for taking lake trout in Lake Superior," by Richard L. Pycha. Accepted for publication in the Journal of the Fisheries Research Board of Canada.

have taken place in nylon twine since it first was introduced. Finally, changes of fishing habits—the tendency for the reduced numbers of fishermen to concentrate their operations on the best grounds during the best seasons—have reduced the dependability of data, particularly on the lake trout fishery of Lake Superior.

The fact must be accepted, therefore, that gill-net statistics are now to a considerable degree undependable for comparisons with earlier fishing and have been for a number of years. It is known that estimates of abundance based on them have been too high. The opinion can be offered that the overestimates are between twofold and threefold in a number of situations, but precise adjustments are not feasible. At such time as the major gill-net fisheries become better stabilized, new base periods can be established to follow changes but the exact relation of the new base level to the earlier one will be unknown and the interpretation of the statistics over considerable stretches of time will continue to be uncertain.

CATCH WITHOUT RECORDS OF EFFORT

The earlier statistical reports included numbers that indicated the kind of gear fished but lacked usable records of the amount. As fishermen became better acquainted with the reporting system and inspection of reports in the original offices of receipt grew more effective, the numbers of defective reports declined to unimportance. Even today, however, a few escape detection up to the point of final tabulation. The system of treatment of these "no-gear-data" catches is accordingly explained briefly by means of the example in table 4.

Table 4.—Illustration of procedure for adjustment of fishing effort to compensate for catches of fishermen whose reports lacked usable data on the amount of gear

[See text for explanation]

Total annual catch	
With gear data	97,310
No gear data	8,432
Grand total	105,742
Recorded effort (E)	3,110
Catch per unit effort (CPE)	31.29
Corrected effort (CE)	3,379

A gear took 97,310 pounds of fish for which usable records of effort were carried on the reports. The CPE for this part of the catch was 97,310/3,110 = 31.29 pounds. The same gear, however, took 8,432 pounds for which gear records were lacking, to bring the total catch to 105,742 pounds. It is estimated then that if all operators who fished the gear had submitted complete reports the true or "corrected" effort (CE) would have been 105,742/31.29 = 3,379. The correction is made on the assumption that fishermen who submitted defective reports caught fish at the same rate (same CPE) as those who turned in usable records.

EFFECTS OF CHANGES IN REGULATIONS

Almost any change of regulation bearing on grounds open to fishing, gear, size limits, or seasons produces an interruption in continuity that hampers comparisons of statistics for years preceding and following the change. If the change becomes effective during the fishing season, the year of change falls into still another category. A lowering of the size limit, for example, suddenly makes available a segment of the stock that previously could not be landed. The catch per unit effort is increased, but the higher abundance index does not reflect a corresponding increase of abundance over that of previous years. Fishing intensity is underestimated under the new lower size limit since the base-period values for CPE were derived in part or wholly on the data for years in which the limit was higher. Similar effects of other changes of regulation are so obvious as not to require illustration or explanation.

A full listing of the changes that have taken place in Great Lakes fishery regulations over the years since the present statistical system was established, could serve no purpose here. Among those that have affected State of Michigan statistics most severely have been: restriction of deep trap nets in Lake Huron to depths of 80 feet or less; a series of changes in the minimum mesh size for small-mesh gill nets (Hile and Buettner, 1955, reviewed the problem of these changes for chub gill nets in Lake Michigan); decrease in size limit for yellow perch from 9 to 8 1/2 inches; two changes of size limit for walleye; change of size limit of whitefish from 2 pounds (equivalent generally to a total length of 18 to 18 1/2 inches) to 17 inches; various changes of closed seasons and particularly the elimination of any closed season on yellow perch in Saginaw Bay (MH-4).

Recent modifications of fishery regulations have been

sweeping in Lake Erie—especially in New York, Pennsylvania, and Ontario—where many size limits have been lowered or eliminated and restrictions on mesh size eased or dropped altogether.

The immediate effects of a change of closed season can, of course, be determined readily by a time-stratification of records. If the change of season involves fractions of months, special tabulations of data are required. It is not feasible usually to obtain the information to measure the effects on the statistics of other changes of regulations. No agency engaged in research on the Great Lakes is in position to carry out the intensive, detailed studies to obtain a sound solution to the problem. For any change, knowledge of the immediate effects can have only limited value since the stocks themselves are modified in response to the new method of exploitation. Comparisons between years, before the change and after the change thus become uncertain. Changes of regulations must be accepted, therefore, as disruptive of the continuity of statistical records and appropriate discretion must be exercised in interpretations.

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The Growth Rate of New England Pollock

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The Growth Rate of New England Pollock

The scales and fork lengths of 299 American pollock (*Pollachius virens* Linnaeus) from seven locations in the Gulf of Maine (Table 1) were analyzed to determine the growth rate. The fish length-scale length ratio was calculated from the average of 3 scale lengths from each of 224 fish. There were less than 3 measurable scales available from the other 75 fish. Plastic impressions of the scales were read and measured on an Eberbach-type projector with a magnification of 43×. Three scales from each fish were measured from the focus to the posterior edge, an average scale length obtained for each fish, and a body-scale regression line computed. The regression equation, $Y = 3.09X + 40.7$, where Y equals fish length in millimeters, and X equals projected scale length in millimeters, was used to back-calculate fish lengths at time of annulus formation. The coefficient of correlation for this regression line is very highly significant, 0.864 ($r = 0.181$ at the 1-percent level, 200 degrees of freedom). Fish lengths at ages I through XI were back-calculated for 257 fish (Table 2). Forty-two samples were discarded for regenerated or otherwise unreadable scales.

Bigelow and Schroeder (1953) show faster growth for the Gulf of Maine pollock from age III to V than we found. Otherwise, the two growth curves are very similar. Growth rates of European populations (Damas, 1909; Wollebaek, 1900) agree quite closely with our results; however, Rojo's (1955) growth rate for pollock of the southwestern Grand Banks differs substantially. Apparently, the Grand Banks pollock grow faster than the pollock of the Gulf of Maine.

TABLE 1.—*Origin of pollock samples*

Locality	Date	Number of fish
Northern edge area of Georges Bank	July 1960	202
South Channel area of Georges Bank	May 1947	67
South Channel area of Georges Bank	March 1960	5
East end of the Cape Cod Canal	July 1960	13[1]
Ipswich Bay, Massachusetts	July 1960	2
Nauset Beach, Massachusetts, 3 to 7 miles offshore	July 1960	4
Stellwagen Bank and off Provincetown, Massachusetts	July 1960	6
Total		299

[1] This sample was taken by hook and line; all others were captured by otter trawl.

TABLE 2.—*Back-calculated length (millimeters) of 257 pollock at annulus formation*

Age group	Number of fish	Annuli										
		1	2	3	4	5	6	7	8	9	10	11
II	9	220	345									
III	22	197	314	428								
IV	62	184	311	423	513							
V	86	181	294	409	508	583						
VI	45	182	292	401	494	571	624					
VII	23	195	300	407	499	578	645	694				
VIII+[1]	10	184	292	391	475	537	605	661	706	726	720	744
Weighted average		192	307	410	498	567	625	678				

[1] All fish older than age group VII are combined in the single category of VIII+ because of the small number of individuals involved.

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TUNA HARVEST

Gerald V. Howard

TUNA HARVEST

Gerald V. Howard, Director of the Bureau of Commercial Fisheries Biological Laboratory, San Diego, California, is the author of this brilliant article on the major world tuna fisheries, and the illustrations are by Richard L. McNeely of the U.S. Bureau of Commercial Fisheries, Seattle, Washington.

TUNAS have long supported important fisheries in the world's tropical and subtropical seas, the tuna fisheries of the Mediterranean and the Japanese Home Islands being of great antiquity. More than a dozen species are caught around the world, the most important being yellowfin, skipjack, albacore, bigeye and bluefin, which common names do not necessarily describe five homogeneous species but, rather, each is a composite of very closely related forms. They are characteristically fishes of similar habits and appearance but vary widely in size although each is commonly represented in commercial landings by specimens of less than 10 lb. Skipjack rarely exceed 25 lb. and few albacore heavier than 60 to 70 lb. are captured, the other three attaining much greater weight. Yellowfin and bigeye as large as 300 lb. are not uncommon and bluefin are frequently even heavier.

The predaceous tunas live in the warm upper layer of the oceans, generally spending all their life far from large land masses, their distribution and migrations being related to changing features of the oceanic environment. Even the so-called subsurface species of certain tropical regions are found in the uppermost 100 fathoms. What is known of their world-wide distribution largely comes from the location and volume of commercial catches.

Areas of commercial fishing are outlined schematically in accompanying charts, as are the average winter and summer positions of the 20° C. sea surface isotherm in the northern and southern hemispheres. Three of the five important species—yellowfin, skipjack and bigeye—are tropical in occurrence and are only found in quantities where water is 20° C. or warmer although skipjack sometimes appear in somewhat cooler water, occasionally in temperatures as low as 15° C. The tropical species respond directly to seasonal temperature changes at the extremes of their ranges and in summers, when the corresponding warm isotherms move unusually far north in the northern hemisphere or south in the southern hemisphere, so do these fish.

Albacore and bluefin are often referred to as the temperate tunas. During summer and autumn, particularly in the earlier years of their life, they are found well to the north or south of the 20° C. isotherm, depending on the hemisphere, as witnessed by such seasonal fisheries as those for albacore in the Bay of Biscay, off the east coast of Japan, and the west coast of the United States, and the bluefin fisheries of the North Sea, California, and south-eastern Australia. Both albacore and bluefin of older age groups are caught the year around in tropical waters of the western and central Pacific, the Indian Ocean, and the south Atlantic, and there is evidence that spawning occurs in these regions.

Within the limits of their temperature tolerance, distribution of the tunas is complex and often varies markedly from month to month and from year to year. It appears to be related primarily to shifting features in the oceanic environment and researchers of the important tuna fishing nations are just beginning to understand this relationship.

Certainly, one important factor is food for tunas are usually found in greatest abundance in regions of high biological productivity. Good feeding conditions coincide with areas of the ocean where the circulation brings nutrient-rich deeper waters into the layer of light penetration. Here, production of phytoplankton is stimulated which, in turn, leads to large crops of forage organisms and, finally, to the concentration of tunas. Variations, within and between years, in the intensity and location of centres of enrichment are known to be an important factor responsible for changes in distribution and relative abundance.

Landings

Although tuna fishing is conducted by almost every maritime country bordering tropical and temperature waters, the tuna fisheries, since the advent of powered boats, have been dominated by Japan and the United States. World landings amounted to just over half a billion pounds (250,000 short tons) in 1948, a billion pounds in 1953, and a billion and one-half in 1957. They may approach 1·8 billion in 1961.

Japan and the United States presently account for more than 90 per cent. of the catch. Japan produces over 70 per cent. of the total, presently worth over 150 million dollars annually to her fishermen and her most valuable fishery. U.S. landings are valued at 45 million dollars and are second to shrimp in value. Other important producers are Peru, France and Spain.

California tuna iner setting her net full speed.

Japan, rather than the United States, has been ponsible for the dramatic increase in world production er the past decade for with the end of the Occupation 1952, Japanese tuna vessels quickly spread their ivities from around the Home Islands into the western, ntral, and south Pacific, and the Indian Ocean. In 56, they moved into the Atlantic and, more recently, ere has been some Japanese fishing in the eastern pical Pacific. Now Japan's tuna fleets range over all e world's tropical and subtropical seas.

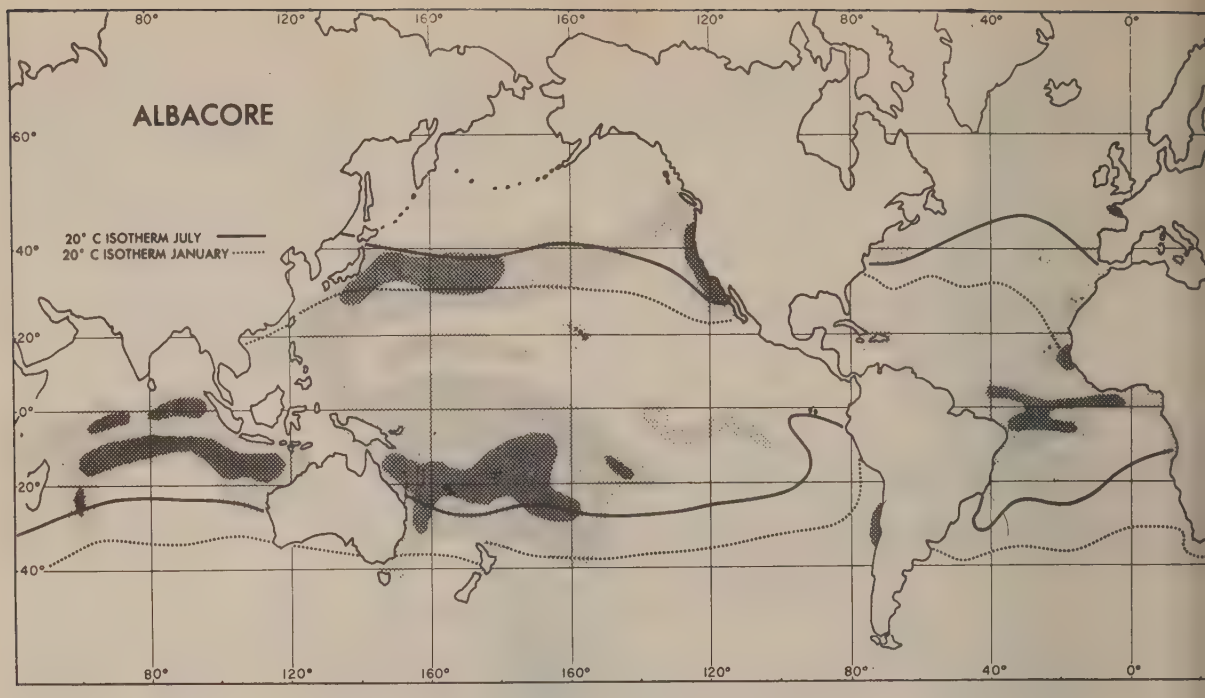
United States production reached a peak in 1950 when 0 million pounds were landed. Since then foreign mpetition, through increasingly heavy tuna imports, lted expansion and the annual catch has stabilized at ll over 300 million pounds. The United States fishery is ncentrated in the eastern Pacific, extending from egon to northern Chile and offshore several hundred iles, but recently, a few vessels have operated in the stern tropical Atlantic. Only minor attention is given to na fishing off the United States East and Gulf Coasts. Tropical species account for three-quarters of the world na catch. Albacore is somewhat more important than uefin in the temperate catch. Until 1960, the United ates tropical fleet caught about equal quantities of ipjack and yellowfin, with the latter presently dominat-g. Very little bigeye is caught by United States hermen. The Japanese, because of the great skipjack hery off the Home Islands, catch nearly as much skipjack they do combined quantities of yellowfin and bigeye.

It is difficult to identify the catch by oceans since tailed information is published by country of origin with record of the ocean from which the catch was taken. owever, the Pacific and Indian Oceans contribute a greater amount than does the Atlantic, where the tropical fishery is of recent origin, and together were responsible for about 80 per cent. of the landings in 1961.

Fishing Methods

A variety of methods is used to capture tuna. Traps, of ancient use but of minor importance, are used in Europe, notably along parts of the Mediterranean coast, and in Japan for bluefin, but are effective only in a few locations where the bluefin seasonally migrate close to shore. Trolling is important for albacore in the Bay of Biscay and off the United States west coast but live-bait fishing, long-lining, and purse seining account for nearly all tropical catches. Long-line fishing is responsible for the total Japanese distant high seas catch, except for skipjack for which live-bait fishing is used. The live-bait method also accounts for one-third of the United States albacore, the bulk of the Japanese Home Islands spring and summer albacore, and, until recently, about 80 per cent. of the United States tropical landings. Purse seining is used for bluefin off California and the coast of Japan and suddenly has become the dominant method in the year-around United States tropical fishery.

In long-line fishing numerous baited hooks are lowered to desired depths. Two main types are used, one for subsurface fishing at depths of 100 to 200 ft., and the other for depths of 150 to 350 ft. The former is used generally for albacore and bigeye, and the latter for bluefin, bigeye and yellowfin. The basic unit of gear is the " basket "—a length of main line, varying in length from 800 to 2,000 ft., to which branch lines, or droppers, are suspended at intervals. Branch lines consist of a cotton section and a wire leader to which a baited hook is fastened. The main line is suspended horizontally by float lines equipped with glass buoys with bamboo flag poles serving as markers between baskets. Long-line vessels vary in size from less



World wide distribution of the Albacore tuna indicated by the commercial fishing activities. Regions of heavy fishing are shaded the darkest. Shown also are the average locations of the 20° C Isotherms during summer and winter.

than 100 gross tons to more than 1,000 tons. Larger vessels set out, each morning, several hundred baskets of gear stretching over many miles of open sea and spend the remainder of the day and part of the night retrieving the catch.

Live-bait fishing methods have changed little over the years. After a supply of live bait (usually small anchovy or herring-like fishes) is obtained inshore and placed in wells aboard, the bait boat proceeds to the fishing grounds. When a school is intercepted, live bait is thrown overboard to attract the tuna close to the vessel. Fishermen then station themselves in racks which hang close to the water. When the school responds to the bait, the tuna become wildly excited in their feeding reaction and strike the feathered jigs, or baited barbless hooks, used by the fishermen. Their lines are attached to short bamboo poles. Disadvantages of the method are that much time is spent catching live bait and there are problems in keeping it alive aboard ship.

United States purse seiners use the one-boat system where the net is carried aboard the catcher-vessel. To surround a school, the large vessel releases a small auxiliary boat, called a " skiff," which is attached to the end of the net. The skiff tows away from the seiner as the latter circles the fish, the seiner joins together with the skiff as the circle is completed and the net is pursed. The net is then pulled aboard until the fish are concentrated for brailing. Tuna seines typically measure 400 to 500 fathoms long by 40 to 50 fathoms deep.

Purse seining is more widely practised by United States fishermen than by others. It began after World War I and, for years prior to 1958, seiners consistently accounted for about 20 per cent. of the tropical tuna and all bluefin landed. Then suddenly in the latter part of 1958, there began a mass conversion of the California baitboa to seiners. The conversion took place at an unprece rate and by 1961 practically all suitable baitboa had been converted. Almost overnight, purse displaced baitboats as the dominant element United States tropical tuna fishery. The event ma have a profound effect on high seas seining thro the world.

The mass conversion was brought about by the duction of the all-nylon net and the power-operated for recovering the seine. The main advantage of the block is the time saved in making sets, parti unsuccessful ones which account for about half of th and now take an hour instead of two. Nylon n handled more easily, need less care and do not dete as rapidly as do cotton nets.

The converted baitboats turned out to be abou as efficient as before and this was a tremendous stim the United States tuna boat owners who had exper marginal profits, but often losses, between 1953 and and to fishermen who had seen their earnings slum employment opportunities drop. This occurred the fact that American fishermen were, even at tha operating much more efficiently than their competitors in terms of catch-per-man-day at sea. ever, the margin of efficiency had not been enou offset differences in living standards. Thanks to th improvements, they are again competitive and tuna are rising with the increasing world-wide demand. theless, United States fishermen are not resting easi they realize they must keep ahead of their comp if they are to remain in business. They know th become more demanding as more and more nations t tuna fishing.

California tuna seiner Cape Beverly was built in 1950 *as a bailboat and converted in* 1960. *Built of wood, she is* 102 *feet overall, carries a crew of* 12, *and has a seine of* 430 × 38 *fathoms hauled by hydraulically - operated power block. Carrying capacity is* 190 *tons. California seiners vary in capacity between* 60 *and* 800 *tons with an average being about* 250 *tons.*

.tistics are essential; not much can be inferred from
le alone.

There are data on catch-per-unit-of-effort for many
na fishing regions but, among the major fisheries, only
at of the eastern tropical Pacific is adequately
cumentec This is an alarming situation when one
nsiders the rapid and tremendous development of tuna
hing now underway throughout the world. Without
oper statistics, if over-fishing occurs, it will not be
tected until too late. Rather, reduced total catch and
wer catch-per-unit-of-effort will likely be excused on the
sis that natural fluctuations are responsible. This is
t to deny that the latter occur but to suggest that they
e too often blamed for decreasing total catch, for we see
ore fluctuations " down " than " up."

The situation in the eastern tropical Pacific, as revealed
the Tuna Commission's analysis of detailed catch and
fort data, is this: the skipjack population is very large
relation to the present harvest, so large that the present
hing intensity is having little or no effect on the average
pulation abundance. For yellowfin, things are quite
fferent. Catch and effort data show conclusively that
ie yellowfin population responds sharply to changes in
hing intensity. The average annual maximum
stainable catch is estimated to lie between 160 and 220 million pounds, with 194 million being the most probable amount. The total yellowfin catch approximated 233 million pounds in 1960 and is expected to exceed that amount in 1961. The Tuna Commission has recently recommended to its member nations (the United States, Costa Rica, Ecuador and Panama) a quota for the yellowfin catch in 1962.

Members of the industry are aware that a yellowfin quota will require adjustments in their eastern tropical Pacific operations, but some see these problems as being easier to solve than those which would arise from the alternative situation—over-fishing. They recognize that regulations will be based on sound scientific principles that are the result of many years of careful research. It is hoped that fishermen in other parts of the world will be as fortunate when the need arises for management of their tuna fisheries.

The world's tuna fisheries have reached maturity. Nations harvesting these great resources now have a joint responsibility to insure that these valuable fisheries flourish and perpetuate themselves. Our growing populations will need more and more food from the ocean. It is necessary that the maximum sustainable harvest of all our great fishery resources be determined and it is essential that this should not be exceeded.

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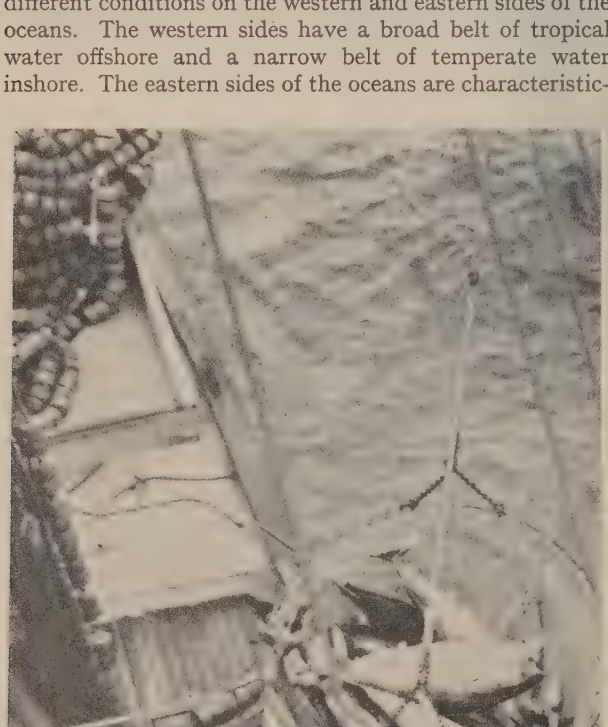
Current Systems

The limitations and advantages of the various fishing methods are related to the distribution and behaviour of the several tuna species which, in turn, are related to features of the environment. Some remarks about the major current systems of the oceans may be helpful in understanding the distribution of tuna and the application of the more important methods.

In equatorial regions, there is a westward transport of surface water north and south of the equator by the North and South Equatorial Currents. These currents turn poleward at their western boundaries, transporting large volumes of warm water into temperate latitudes. In the northern hemisphere, between 30° and 40° N., these currents leave the shore and flow north-easterly, joining the cold counter-clockwise currents, the Oyashio in the Pacific and the Labrador in the Atlantic, and proceed eastward. Processes of mixing and cooling during the eastward flow are such that, when the waters reach the western shores, or eastern side of the ocean, they are no longer tropical. The southward-flowing California and Canary Currents transport cool water well into the tropics where they swing offshore into the equatorial region, completing the circle.

The circulation described gives rise to substantially different conditions on the western and eastern sides of the oceans. The western sides have a broad belt of tropical water offshore and a narrow belt of temperate water inshore. The eastern sides of the oceans are characteristic-



Hoisting aboard a brail full of tuna from "dried-up" bag of seine net.

ally the opposite. The tropical ocean, simply stated two-layer system of persistent stability. The upper is referred to as the mixed layer because it is isothe This is where the tuna live. The mixed layer is war is separated from the cold water of the depths by a s thermocline, or sharp temperature gradient. differences described for the eastern and western sid the oceans profoundly affect the thickness of the upper mixed layer. In the eastern portion of the tr oceans, the mixed layer is thin, from 50 to 200 ft. on the western side, it is much thicker, frequently than 300 ft.

The use and effectiveness of the principal types of fi gear for yellowfin and bigeye tuna are directly relat the depth of the upper mixed layer. The eastern ma of the tropical oceans are the only areas where live-bait and purse seine fisheries for these species the year around. Live-bait fishing and purse se depend on these tunas being near the surface. The line method, which was the basis of the great Jap expansion in tuna fishing in the 1950's, is the only m presently available which is successful in catching yell and bigeye in the tropics where the mixed layer is These fishes penetrate the entire range of the d mixed layer of central and western tropical oceans.

The skipjack behaves differently. Apparent remains close to the surface, whether the mixed lay deep or shallow. This appears to be the reason tha long-line gear is not effective in its capture. Catch skipjack in the areas of the great tropical Jap long-line fisheries for yellowfin and bigeye are so sma so scattered that they only provide evidence of occurrence. Live-bait fishing probably would be effe for skipjack in the vast high seas regions of the tropic is limited by the need for small bait fishes usually fou catchable quantity only close to land. Purse se techniques have not been tried extensively on the moving skipjack schools in the central and western tr oceans.

Condition of Resources

When one considers that the major tuna fisheries for a considerable period, ranked high among the w fisheries, it is surprising that, as recently as a decade knowledge of the biology, life history, ecology and of commercial fishing on the populations of the se species was almost completely lacking. Some res programmes during the last 10 years, notably the prehensive programme of the Inter-American Tr Tuna Commission in the eastern tropical Pacific and of the United States Bureau of Commercial Fish Biological Laboratory, Honolulu, have made progress towards elucidating the ways of these mercially important fishes.

For studying the effect of the commercial harve fish populations and determining their maxi sustainable harvest, knowledge is needed of the history and ecology of the species concerned. Fur more, accurate and detailed catch and effort statistic required. Most needed are measures of total catch, fishing effort, and catch-per-unit-of-effort over a ser years at different levels of fishing intensity. All

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Sea Temperatures and the Availability of Albacore off the Coasts of Oregon and Washington[1]

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ABSTRACT

Wide variations exist in landings of albacore (*Thunnus germo*)[2] in Oregon and Washington. In 1944, Oregon and Washington landings reached 34 million pounds, but dropped to 0.6 million pounds a decade later. Variations in landings may be a result of fluctuations in availability. Distribution of albacore along the North American coast is known to be influenced by sea temperatures. Although weather conditions and economic factors are reflected in Oregon–Washington landing statistics, it may be that annual variations in sea surface temperatures are also affecting the success of the fishery by varying availability to the fishermen.

Relationship between sea surface temperatures and landings was investigated for the years 1947–60. In years of above-normal temperatures, landings were, in general, significantly greater than in years of below-normal temperatures. Whereas warm water did not insure a good fishery, widespread cold water was detrimental to success of the fishery. The data suggest that in June, if the sea temperature anomaly is large enough, it is possible to predict whether or not sea temperatures will be favorable for albacore at normal time of commencement of the fishery in mid-July.

INTRODUCTION

Albacore (*Thunnus germo*) of the north Pacific Ocean range from Japan to North America. In June of each year this species usually appears in North American coastal waters, and shortly thereafter a commercial fishery occurs which frequently lasts through the remainder of the year. Commercial fishermen have taken albacore from southern Baja California to Alaska, but since 1945 the majority of the fish have been caught in an area between Baja California and San Francisco, within 400 miles of the coast (Clemens, 1955).

Although albacore have been taken commercially off California since the early part of this century, it was not until 1937 that a fishery developed off the Oregon–Washington coast. Throughout the history of the fishery in the coastal waters of North America, fluctuations in landings have been marked. Landings in California never exceeded 0.7 million pounds from 1928 to 1934, but 31 million pounds were landed in 1917, and 62 million pounds were landed in 1950 (California. Bureau of Marine Fisheries, 1949 and 1952). In 1944 Oregon and Washington landings reached 34 million pounds, but dropped to a low of 0.6 million pounds a decade later (*Pacific Fisherman Yearbooks*, 1950 and 1961). Success of the fishery in coastal waters of these states does not appear to be related to success of the fishery off California.

Fluctuations in landings of albacore appear to be the result of yearly variations in abundance and variations in availability rather than fishing, although no concentrated studies have been made concerning the effect of fishing on the population. Marr (1951) has defined availability as the degree to which a population is accessible to the efforts of a fishery. He suggested that, for fisheries carried out over only a portion of the migratory route of a species, it might be expected that variations in availability would often be more important than variations in abundance in determining the yield. Because the Oregon–Washington fishery is carried out over a small range both in time and in area of the migratory route of the albacore, it is likely that in this fishery the annual variations in availability are as important or are more important than changes in abundance.

Distribution of albacore along the North American coast is influenced by sea temperatures (Hubbs and Schultz, 1929; Radovich, 1961). Although weather conditions and economic factors are certainly reflected in Oregon–Washington landing statistics, it may

[1] Paper presented at the Pacific Tuna Biology Conference, August 1961, Honolulu, Hawaii.

[2] Proper application of the name depends on whether or not the Pacific form *germo* is distinct from the Atlantic *alalunga*. This will be discussed at the FAO World Tuna Conference to be held at La Jolla, California, July 2–14, 1962.

TABLE 1.—*Pounds of albacore landed in Oregon and Washington by month from 1947–1960*[1]

Year	July	August	September	October	November	December	Total
1947	2,303,505	5,296,515	4,482,639	1,186,212	–	–	13,268,8
1948	4,505,801	7,868,062	1,703,144	215,731	–	–	14,292,7
1949	1,401,712	5,317,560	2,520,998	1,489,042	31,529	–	10,760,8
1950	3,819,132	3,967,902	537,937	1,239,970	210,851	–	9,775,7
1951	95,145	345,350	1,529,702	1,366,233	101,604	–	3,438,0
1952	14,509	128,738	1,353,412	929,881	278,774	57,103	2,762,4
1953	–	21,998	569,765	217,583	–	–	809,3
1954	–	–	108,069	450,161	36,222	13,231	607,6
1955	–	–	26,881	518,211	158,212	–	703,3
1956	–	501,185	3,004,101	595,192	173,643	9,128	4,283,2
1957	94,468	1,038,214	700,663	1,193,373	32,193	–	3,058,9
1958	415,892	6,385,464	3,163,198	161,607	–	–	10,126,1
1959	1,881,881	6,009,548	4,798,162	120,970	–	–	12,810,5
1960	23,007	1,184,072	2,772,417	47,965	–	–	4,027,4
Total	14,555,052	38,064,608	27,271,088	9,732,131	1,023,028	79,462	90,725,3

[1] Source—*Pacific Fisherman Yearbook* (1950, 1959, 1960, and 1961). Total landings for 1958 and 1959 appro mately 10 percent higher as reported by 1961 *Yearbook*, but monthly breakdown available only for statistics given h obtained from 1959 and 1960 *Yearbooks*.

be that annual variations in sea surface temperatures are also affecting the success of the fishery by varying availability to the fisherman.

It is the objective here to evaluate the relationship between oceanic temperatures off Oregon and Washington and landings of albacore in these states, and to provide evidence that sea surface temperatures are a useful index for predicting seasonal availability of albacore in the coastal waters of the Pacific northwest.

SOURCES OF SEA TEMPERATURE AND LANDING DATA

The Bureau of Commercial Fisheries Biological Laboratory, Stanford, California, is investigating broad-scale temperature changes in the Pacific Ocean. Oceanographic and marine meteorological data have been obtained by that laboratory from the National Weather Records Center, Asheville, North Carolina, for the region of the Pacific Ocean north of 20° S. latitude. Monthly summaries of injection temperatures taken by merchant and naval ships by 2-degree squares were made available to the author, and were used to compute 12-year (1947–58) monthly means, which in turn were used as a base to chart monthly sea temperature anomalies from 1947 to 1960. Data for 1959 and 1960 were not available at the time of construction of the monthly mean charts, and data prior to 1947 were too few to warrant analysis.

Injection temperatures are subject to variable errors due to type, placement, and operation of injection systems which vary widely from ship to ship, and because commerci grade thermometers are used in the syste Intakes for injection systems are appro mately 10–30 feet below the surface of t water; in oceanic areas temperatures o tained from these systems are essentially s face temperatures.

Landing statistics were extracted from *P cific Fisherman Yearbook* (1950, 1959, 196 and 1961). For the years 1947–60, 90,725,3 pounds of albacore were landed in Washi ton and Oregon. An additional 9,442,2 pounds caught in the Northwest were land in British Columbia and California (dete mined from various California Department Fish and Game Bulletins and personal co munication from J. C. Stevenson of the D partment of Fisheries, Canada), but the data were not readily available by month f the 14-year period and have not been i cluded in the analysis.

RESULTS AND DISCUSSION

The Oregon–Washington albacore fishe is conducted by troller and live-bait boa Purse seining has been tried from time time without apparent success. The fishery generally conducted within 200 miles of t coast, begins around mid-July, reaches peak in August and September, and term nates in October or November.

Approximately 40 percent of Orego Washington albacore landings over the pa 14 years have occurred in August (Table 1 Success of the fishery each year correspon generally to success achieved during Augus for this reason August sea temperatures a

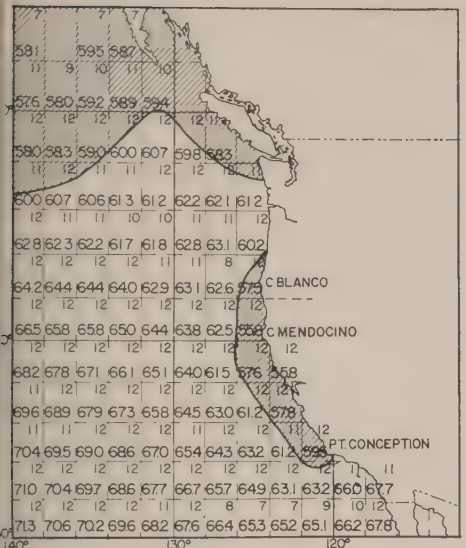

FIGURE 1.—Average sea surface temperatures (°F.) by 2-degree squares in the northeastern Pacific Ocean for August, based on injection temperature readings for twelve years (1947–58). Number in upper right hand corner of each 2-degree square indicates the number of years that were used in making the average. Shaded portions denote areas having average temperatures less than 60° F.

anomalies are used in year-to-year comparisons with total landings.

Movement of albacore off the North American west coast has been associated with the northward movement of the 59° F. isotherm (Johnson, 1960). Alverson (1961) has shown that research vessels operating in oceanic water off Oregon and Washington obtained best fishing rates in approximately 60° F. water. For a normal August, based on the 12-year period 1947–58, the 60° F. isotherm at its most northern penetration is at about 50° N. latitude and 130° W. longitude (Figure 1). In warm years this isotherm may penetrate to the north side of the Gulf of Alaska, and in cold years it may reach no farther north than 46° N. latitude at about 130° W. longitude.

Yearly landings can be readily divided into above-average periods (1947–50, 1958–59) and below-average periods (1951–57, 1960) (Figure 2). August ocean temperatures (average of 2-degree square temperatures in the area from 40° to 50° N. latitude, and from the west coast of North America to 130° W. longitude) followed a similar pattern (Figure 2).

In 1947 and 1948, August sea temperatures off Oregon and Washington were above average (Figures 2 and 3). Landings for these years were well above the 14-year average. In 1949 and 1950, sea temperatures were slightly lower, and, correspondingly, landings were down. The next 5 years were plainly "cold water" years, and landings during these years were significantly below average. In fact, in 1954 and 1955, albacore were not landed until September (Table 1), and then only in small amounts. A warming trend began in 1956, and landings, although still below average, were the highest since 1950. That water much warmer than normal prevailed off the North American coast in 1957 and 1958 is well documented by Stewart, *et al.* (1958), Reid (1960), and others. Albacore landings in 1958 were the highest since 1949. In 1957, however, even though warm water was widespread in the area of the fishery (Figure 3), landings were significantly below average. Of the 14 years studied here, 1957 is least compatible with the suggestion that warm water is normally accompanied by good albacore fishing.

It is noteworthy that economic conditions may have contributed to the decline in landings in 1957. Imports of albacore from Japan in 1956 and 1957 caused a serious glut in the United States albacore market. Price paid to domestic fishermen in 1957 dropped considerably, and for a time canners were not purchasing albacore from the domestic fleet.[3]

Based on comparisons of sea temperatures and landings from 1951 to 1957, it is suggested that warm water does not always indicate good fishing, but cold water is usually detrimental to the fishery. Warm water remained widespread in 1959, and landings were the highest since 1948. Cold water returned by 1960, and, accordingly, landings were down significantly.

Pre-season predictions on the availability of albacore would be of considerable economic importance to the industry. With this

[3] Personal communication from W. M. Chapman of the Resources Committee, San Diego, California

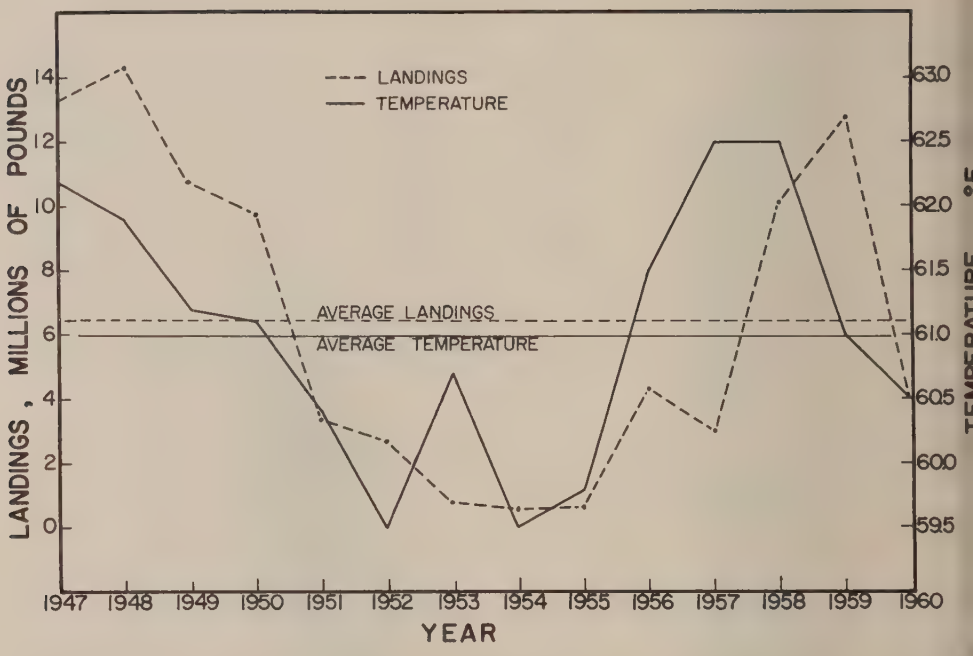

FIGURE 2.—Average sea surface temperatures for August for the oceanic area from 40° to 50° N. latitud and from the west coast of North America to 130° W. longitude for the years 1947 to 1960, and total landing of albacore in Oregon and Washington for the same years.

in mind, correlation coefficients were computed between average surface temperatures in March through August and total landings. The following positive values were obtained: March, 0.32; April, 0.57; May, 0.34; June, 0.46; July, 0.60; and August, 0.62. Clearly a trend is evident toward increasing significance through August. April, July, and August correlations are significant at the 5 percent level. The coefficients indicate that predictions of sea surface temperatures would be useful in predicting albacore availability.

Sea temperatures depend on ocean circulation and energy exchanges at the air–sea interface, but oceanographers have been generally unsuccessful in determining which of these processes has the most influence in open ocean areas. It seems likely that the relative importance of the two processes varies both spatially and temporally.

Circulation in the North Pacific is dominated by an eastward-flowing current which divides off the American coast to form the Alaska Gyral and the California Current (Sverdrup *et al.*, 1942). The shifting of this zone of division probably determines th character of the albacore water off Orego and Washington. According to Barnes an Paquette (1954), the splitting occurs in a ill-defined zone well offshore at approxi mately 45° N. latitude, both orientation an position of the zone of divergence varyin with season. Fleming (1955) notes that i summer the split occurs at about 50° N. lat tude, and in winter shifts southward to abou 43° N. latitude. A non-seasonal southerl shift of this zone of division appears to hav caused an anomalous intrusion of warm wa ter in 1957 and 1958 into the coastal region of Oregon, Washington, and British Colum bia (Tully *et al.*, 1960). Certainly such a event must play a major role in the distribu tion of albacore.

Although accurate predictions of sea su face temperatures ultimately will depend o knowledge of both advective processes an energy exchanges at the air–sea boundary there appears to be some merit in predictin temperatures on the basis of assuming per sistence of anomalies alone, especially if th

FIGURE 3.—Sea surface temperature anomalies during August 1947–60 for the region from 40° to 50° N. latitude and from the west coast of North America to 130° W. longitude. Anomalies based on 1947–58 mean. Contour interval 2° F. Shaded areas colder than mean.

anomaly is of considerable magnitude. Roden and Groves (1960) concluded that in the northeastern Pacific the best estimates of future temperatures can be made from past observations, and Reid *et al.* (1958) and Robinson (1961) found that major anomalies at stations along the west coast of North America lasted several months. In a study of sea temperatures collected from five light stations, Tabata (1957) also discovered coherence in temperature events; warmer months were followed by warmer months and colder months by colder months. Hester (1961), describing a method of predicting albacore and bluefin catch in certain regions off southern California, found persistence of winter coastal temperature anomalies into the summer.

In this study it was found that if the temperature anomaly offshore from Oregon and Washington was large enough in May and June, it persisted into July and August (Figure 4). In 1947, 1948, 1957, and 1958, years when August temperatures were above the 12-year average, warmer-than-normal water was present at least a month before the fishing season began in mid-July. When lower-than-normal temperatures prevailed in August (1951–55, 1960), low temperatures had prevailed during the preceding two months. In 1949, 1950, and 1956, however, the anomaly changed from cold to warm from July to August.

The use of injection temperatures and the lack of catch-per-unit-effort data necessarily restrict conclusions that can be made from the foregoing analysis. However, the implication that can be drawn from the correlation coefficients and from the persistence of anomalies as shown in Figure 4 is that there is a relationship between sea temperature and availability of albacore, and that predictions of availability on the basis of sea surface temperature anomalies can be made when the anomalies are large enough.

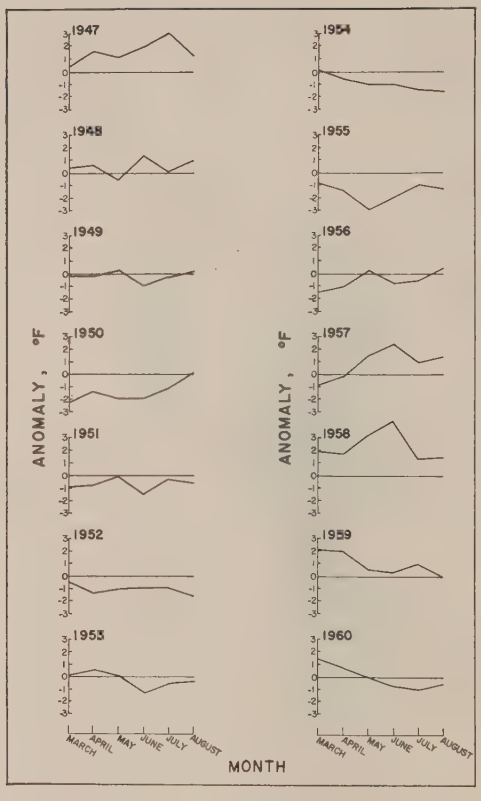

FIGURE 4.—Sea surface temperature anomalies (°F.) from March through August (1947 to 1960) for the area from 40° to 50° N. latitude and from the west coast of North America to 130° W. longitude. Anomalies based on 1947–58 mean.

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EVERET C. JONES

EVIDENCE OF AN ISLAND EFFECT UPON THE STANDING CROP OF ZOOPLANKTON NEAR THE MARQUESAS ISLAND, CENTRAL PACIFIC

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Evidence of an Island Effect upon the Standing Crop of Zooplankton near the Marquesas Islands, Central Pacific

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Introduction

A survey of the literature indicates that a number of authors have attempted to determine the nature of the effect, if any, of oceanic islands on the standing crop of zooplankton or on the productivity of adjacent waters.

HARDY (1928) suggested that the island of South Georgia caused upwelling which brought phosphates to the surface, resulting in higher standing crops of zooplankton and whales near the island. In a later work (HARDY and GUNTHER, 1935) he stated that this hypothesis was wrong, inasmuch as there was always a surplus of phosphates in the surface waters of the entire polar region. He then stated that upwelling may bring other salts or resting spores to the surface. He also considered the possibility that run-off water from the island might bring iron compounds into the sea, which would result, as GRAN (1931) had found, in higher production of phytoplankton.

TOKIOKA (1942) found greater volumes of plankton in areas influenced by waters of littoral characteristics originating in the Palau and Yap Islands than in the North Equatorial Current. He found evidence of littoral influence as far as about 5 miles offshore.

MOORE (1949) considered that the observed distribution of zooplankton around Bermuda might be explained partially by upwelling associated with the islands. JOHNSON (1949) found that the concentration of certain plankters within the lagoon of Bikini was four times that in the outside waters. He attributed this primarily to reduction in dispersal and secondarily to a possibly higher level of food production within the lagoon. EKMAN (1953, page 313) stated that "small oceanic islands act, although to a lesser extent, as coasts" in the collection of mineral nutrients with resultant higher standing crops of plankton.

KING and HIDA (1954) were apparently the first to attempt a statistical test of the relation between the standing crop of zooplankton and distance from oceanic islands. They found no evidence of an island effect near the Hawaiian

Islands. SETTE (1955) suggested that eddies to leeward of the Hawaiian Islands were mechanisms of enrichment, and MCGARY (1955) pointed out that zooplankton maxima were associated with cyclonic eddies in the lee of these islands. Again KING and HIDA (1957 a), however, found "no conclusive evidence of enrichment downstream from the islands as a result of eddy systems, upwelling, land drainage, or other influence of the littoral waters."

DOTY and OGURI (1956) maintained that productivity increases as oceanic islands are approached and presented data which supported their hypothesis on the rates of carbon fixation at various distances from Kaneohe Bay, Oahu. KING and HIDA (1957 b) tested the relationship between the standing crop of zooplankton and the distance from Palmyra Island in the central Pacific and found no gradient from the island to 14 miles offshore.

UDA and ISHINO (1958) tested models of islands of various shapes and found that they produced perturbations which modify the two-layer system. YOUNT (1958) considered that certain observed maxima in the abundance of Salpidae in the central Pacific were related to the proximity of islands. HOLMES and BLACKBURN (1960) presented very limited data, with no conclusions, on the relationship between the standing crop of zooplankton and the distances from Clarion, Clipperton, and Cocos Islands in the eastern Pacific.

BENNET and SCHAEFER (1960) suggested that islands cause changes in the physical circulation or the biochemical cycle resulting in greater supplies of food for tunas in their immediate environs. They surveyed the rate of carbon fixation and the distribution of chlorophyll *a* and zooplankton in the area of Clarion and Socorro Islands and Shimada Bank in the eastern Pacific. In these measurements of productivity and standing crop, no conclusive evidence of an island effect was found.

While examining, for indicator organisms, plankton samples collected in the vicinity of the Marquesas Islands, central equatorial Pacific (see Figure 1), I found (JONES, MS) populations of neritic copepods, *Calanopia* sp. and *Undinula vulgaris* (Dana) var. *typica* Sewell, as far as 80 to 100 nautical miles from the nearest island. These populations of inshore copepods at offshore stations were generally associated with the higher values of standing crop of zooplankton. This association led to the hypothesis that the standing crop of zooplankton increases with decreasing distance from the nearest island of the Marquesas.

Materials

Data used to test this hypothesis consisted of plankton volumes (in ml/1000 m^3 of water strained) and distances obtained from station positions published by WILSON, NAKAMURA, and YOSHIDA (1958) from four offshore surveys: October–November 1957, January–February, March–April, and May 1958. Each survey consisted of a north–south transect and an east-west transect in the form of a cross with the Marquesas Islands grouped around the intersect. Each transect was about 500 nautical miles long. All stations were occupied at night, and the plankton samples were collected with a 1 m net towed obliquely from the surface to 140 m and return (see WILSON *et al.*, 1958, for details of collecting methods). The range of distances from the nearest island was about 10 to 180 miles for each survey. This is in sharp contrast with the previously cited works, in which the maximum distances were about 15 miles. Plankton volumes and distances from the nearest island used in this paper are presented in Table 1.

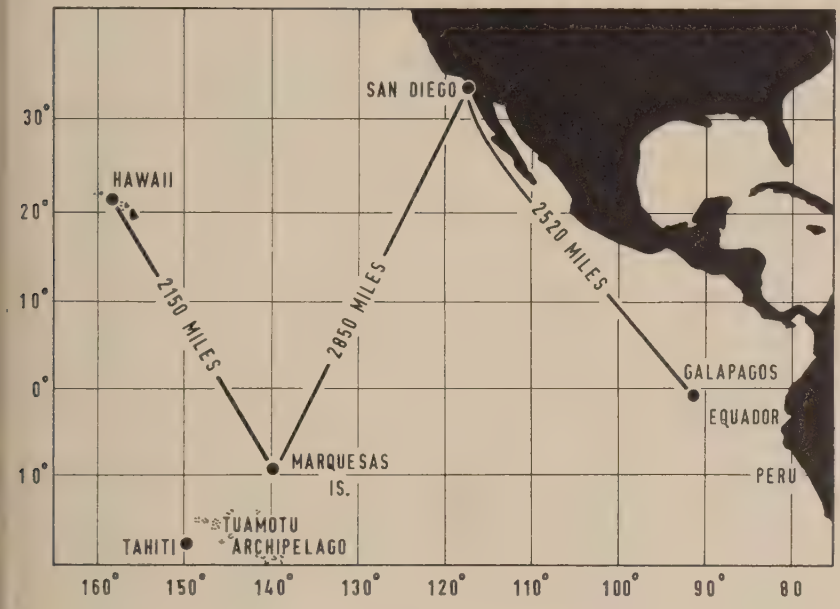

Figure 1. Location of the Marquesas Islands.

Results

Because plankton is thought to be non-randomly distributed, a non-parametric analysis was used. From plankton volumes and distances from the nearest island, SPEARMAN's rank correlation coefficient, r_s, (SIEGEL, 1956) was determined for each of the four surveys:—

Survey	Date	r_s	N	P_{r_s}
R.V. "Charles H. Gilbert" Cruise XXXV...	Oct.–Nov. 1957	−0·455	23	<0·05
R.V. "Hugh M. Smith" Cruise XLIII.....	Jan.–Feb. 1958	−0·478	23	<0·05
R.V. "Charles H. Gilbert" Cruise XXXVIII	Mar.–Apr. 1958	−0·583	24	<0·01
R.V. "Hugh M. Smith" Cruise XLV.....	May 1958	−0·140	20	>0·05

The negative r_s values were significant for three of the four surveys. Therefore, the hypothesis that the standing crop of zooplankton increases with decreasing distance from the nearest island was accepted for three of the surveys and rejected for the fourth, "Hugh M. Smith" Cruise XLV.

To test the hypothesis that this negative correlation of plankton volumes with distance from the nearest island existed in all four cardinal directions from the intersect of the survey transects, the plankton volume and distance data from the four surveys were lumped and then divided into north, east, south, and west legs. SPEARMAN's rank correlation coefficient was determined for each leg:—

Leg	r_s	N	P_{r_s}
North.....	−0·401	21	<0·05
East	−0·422	21	<0·05
South.....	−0·463	21	<0·05
West.....	−0·476	23	<0·05

Table 1

Plankton volumes and distances from the nearest island

Stations[1])	Direction from intercept of transects	Distance in nautical miles from the nearest island	Plankton volumes[2]) in ml/1000 m³
R.V. "Charles H. Gilbert" Cruise XXXV 1957			
35–36	E	70	20
38–38A	E	105	25
38B–39	E	185	19
41–42	E	145	25
44–45	E	25	22
47–48	E	30	42
50–51	S	60	34
53–54	S	70	36
55–56	S	125	38
58–59	S	110	38
60–61	S	20	38
62A–63	N	75	37
65–66	N	85	40[3])
67–68	N	120	24
70–71	N	110	36
73–74	N	20	28
76–77	N	5	63
79–80	W	85	28
82–83	W	110	26
84–85	W	150	33
87–88	W	75	28
90–91	W	30	45
93–94	W	10	63
R.V. "Hugh M. Smith" Cruise XLIII 1958			
30	E	25	65
32	E	35	65
34	E	125	26
36	E	145	35
39	S	25	25
41	S	35	58
42	S	110	15
44	S	135	18
47	S	80	51
49	S	60	98
57	W	55	38
59	W	80	41
60	W	170	54
62	W	120	27
64	W	35	52
66	W	10	35
70	N	60	103
71	N	85	26
73	N	150	33
75	N	110	48
76	N	25	100
78	N	15	69
83	N	25	70

Table 1 (continued)

Stations[1])	Direction from intercept of transects	Distance in nautical miles from the nearest island	Plankton volumes[2]) in ml/1000 m³
R.V. "Charles H. Gilbert" Cruise XXXVIII 1958			
46	E	60	41
48	E	85	55
49	E	160	36
51	E	125	47
53	E	35	79
55	E	12	73
57	N	56	60
59	N	86	35
60	N	142	38
62	N	122	47
64	N	42	102
66	N	10	61
69	W	60	45
71	W	100	43
72	W	165	35
74	W	135	52
75	W	20	48
77	W	15	72
78	S	70	38
80	S	90	37
81	S	138	47
83	S	108	42
84	S	42	70
86	?	14	51
R.V. "Hugh M. Smith" Cruise XLV 1958			
78	E	60	19
79	E	100	20
82	E	165	37
83	E	120	26
84	E	30	34
87	W	70	62
88	W	110	31
90	W	175	30
91	W	130	34
94	W	35	80
97	N	55	25
98	N	125	21
101	N	150	40
102	N	110	24
103	N	30	24
107	S	65	66
108	S	80	15
110	S	145	21
111	S	108	23
113	S	25	76

[1]) The plankton volumes for "Charles H. Gilbert" Cruise XXXV are averages of two samples from each locality.
[2]) Jellies >2 cm in length and other organisms >5 cm in length are not included.
[3]) The plankton volume for "Charles H. Gilbert" Cruise XXXV, Station 65 was recalculated because of an error in the meter reading and therefore differs from that given in WILSON *et al.* (1958).

The negative r_s values for all four legs were significant; therefore, the hypothesis was accepted. Although the value for the western leg was highest, I know of no test for significant differences among r_s values such as the z transformation used to test for significant differences among r values (SNEDECOR, 1946, page 151), so it is not possible for me to determine whether these r_s values are all from the same population. However, the highest correlation, that obtained from the western leg, may be associated with the westerly flow of surface waters in the Marquesas Islands region as indicated by geostrophic considerations and longline drifts (AUSTIN, MS).

That the correlation analyses of the four surveys did not result in fortuitously significant r_s values is borne out by similar tests performed on the variables of Secchi disc readings and distance from the nearest island. These data, also taken from WILSON *et al.* (1958), were analysed by SPEARMAN's rank correlation with the following results:—

Survey	Date	r_s	N	P_{r_s}
R.V. "Charles H. Gilbert" Cruise XXXV...	Oct.–Nov. 1957	−0·588	10	<0·05
R.V. "Hugh M. Smith" Cruise XLIII.....	Jan.–Feb. 1958	−0·633	18	<0·01
R.V. "Charles H. Gilbert" Cruise XXXVIII	Mar.–Apr. 1958	−0·562	13	<0·05
R.V. "Hugh M. Smith" Cruise XLV.....	May 1958	−0·250	17	>0·05

As in the analysis of plankton volumes and distances from islands, three of the four negative r_s values were significant and that of the fourth survey, "Hugh M. Smith" Cruise XLV was not significant. The distances used in this analysis were not identical with those used with plankton volumes, since Secchi disc readings were taken in the daytime and the plankton samples were collected at night. The Secchi disc data were not suitable for division into directional legs as were the plankton volume data.

Discussion

At the present stage of knowledge, any consideration of causative mechanisms is little more than speculation. A brief discussion of some which have been advanced by previous authors and of other possible hypotheses may be of value.

SARGENT and AUSTIN (1949), DOTY (1954), and DOTY and OGURI (1956) have suggested that benthic algae accumulate inorganic nutrients from passing waters, leading to higher standing crops of benthic organisms and, in the opinion of DOTY and OGURI, of plankton communities in adjacent waters. In the Marquesas Islands there is a conspicuous lack of benthic algae or of suitable places for them to grow. Such a condition would seem to preclude the applicability of this hypothesis to those islands.

Qualitative examination of the plankton samples indicated that the higher sample volumes near the Marquesas Islands could not be attributed directly to the bulk of neritic plankters. In most cases the higher volumes were composed largely of euphausiids and siphonophores, neither considered to be land-dependent. Therefore the possibility arises that the higher plankton volumes may be due to some circulatory feature of the ocean not at all connected with the islands. In my work on indicator species in the area (JONES, MS), I found that the southern boundary of the equatorial waters, as indicated by the southern limit of distribution of two species of *Candacia*, *C. pachydactyla* (Dana) and *C. catula* (Giesbrecht), was at about 8° to 11°S, latitudes which correspond to

those of the islands. Thus the islands are located in a boundary zone which may be a mechanism of enrichment (HARDY and GUNTHER, 1935; MCGARY, JONES, and GRAHAM, 1958). However, because the boundary is zonal (east-west), it seems unlikely that such a mechanism would lead to the observed significant correlations on all four directional legs.

Data are not available for determining whether or not perturbations in the circulation are produced by the presence of the Marquesas Islands. Upwelling, eddy formation, convergences, or other disturbances of circulation associated with oceanic islands have been put forward as mechanisms of enrichment, and this possibility cannot be ruled out in the present case.

HARDY and GUNTHER (1935), DOTY and OGURI (1956), and KING and HIDA (1957 a) refer to the possibility that products of run-off water lead to higher productivity in waters adjacent to islands. While nothing in the distribution of surface salinity or phosphates in waters surrounding the Marquesas Islands indicated extensive run-off water, there is the possibility that unmeasured chemical factors such as iron compounds (HARDY and GUNTHER, 1935; GRAN, 1931) may diffuse or be carried by currents from these high islands as a result of leaching by ground water, surface run-off from streams and heavy rains, or abrasion of the coast by wave action. The almost complete absence of fringing reefs or shallows around the Marquesas Islands may contribute to this abrasion and to the diffusion and transport of terrigenous influence to points a considerable distance from land. Such influence seems to be indicated by the occurrence of neritic copepods as far as 80 to 100 nautical miles from the nearest island.

Acknowledgements

I am grateful to Mrs. Betty Ann KEALA for suggesting the method of analysis and for doing the actual calculations.

Summary

1. The hypothesis that the standing crop of zooplankton increases with decreasing distance from the nearest island of the Marquesas, in the distance range of 10 to 180 miles, was tested and significant negative rank correlation coefficients were obtained from three of four surveys made at different seasons. Corroborating evidence that this relationship was not fortuitous was found in tests of rank correlation of Secchi disc readings and distances from the nearest island in which significant negative r_s values were obtained from the same three out of four surveys.

2. When the plankton volume and distance data were lumped and divided into four directional legs, significant negative rank correlation coefficients were obtained from all four legs. That of the western leg was the highest and may be associated with the westerly flow of surface waters in the area.

3. As a causative mechanism, the hypothesis that benthic algae accumulate inorganic nutrients from the passing water and that this leads to higher standing crops of zooplankton in adjacent waters was considered and for the present case rejected, because benthic algae or suitable places for them to grow are largely absent in the Marquesas.

4. The hypothesis that the boundary zone between major oceanographic features in which the Marquesas Islands lie produces enrichment independent of the presence of the islands was considered and rejected because of the correlations west and east of the islands, which are not in agreement with the zonal nature of the boundary zone.

5. The hypothesis that the islands produce perturbations in the adjacent waters leading to enrichment was considered but not tested because of inadequate data.

6. Although the higher volumes of plankton at offshore stations near the islands were composed largely of open ocean forms, the presence of neritic copepods associated with those higher volumes appears to support the hypothesis that terrigenous products diffuse or are carried by currents from the islands and lead to higher productivity of adjacent waters.

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WILDLIFE SURVEYS ALONG THE NORTHWEST COAST OF WASHINGTON

KARL W. KENYON and VICTOR B. SCHEFFER

Reprint from Murrelet 42: 29-37

The purpose of this paper is to report observations of marine birds and mammals in the island wilderness and coastal waters off the Olympic Peninsula. The area covered is about 75 miles north-to-south and 3 miles east-to-west. Considering its proximity to centers of human population, relatively few zoological studies have been undertaken here. From 1914 to 1921 George G. Cantwell, of the Biological Survey, acted as custodian of the Federal bird refuges along the Olympic seacoast and, in his spare time, collected birds and mammals at various places in the lowlands of the peninsula. Scheffer and Macy (1944) made an aerial survey in 1944; and Scheffer and Dalquest made a survey of Destruction Island in 1941 (Dalquest, 1948). We now present data obtained on six aerial surveys from 1949 to 1959 and on a surface survey made by boat and on foot in 1959.

Place names. — By executive order of 23 October 1907, Theodore Roosevelt established three "reserves" or refuges along the outer coast of the Olympic Peninsula. The legal description indicates, more by map than by words, a continuous strip except between Lat. 47° 29′ N. and 47° 38′ N. (a 9-mile break off the Queets River). The northern and southern boundaries are shown as minutes of latitude; the eastern boundary is the coastline; the western boundary is indicated by a dotted line which includes all offshore rocks and islets except Umatilla Reef and Destruction Island. The east-west width of the refuges is about 3 miles. The refuges were established "for the use of the Department of Agriculture as a preserve and breeding ground for native birds and animals" (Roosevelt, 1907). Today they are National Wildlife Refuges, administered by the Bureau of Sport Fisheries and Wildlife, U. S. Fish and Wildlife Service, Department of the Interior. From north to south, they are listed below. See Jewett *et al* (1953, p. 44) for descriptions of these areas.

1. Flattery Rocks National Wildlife Refuge

   From 48° 23′ to 48° 02′ N.; excludes Tatoosh and Umatilla Reef, but includes Spike Rock, Father and Son, Bodelteh Islets (Fig. 1A), Flattery Rocks, Ozette Island (Fig. 1B), and White Rock.

2. Quillayute Needles National Wildlife Refuge

   From 48° 02′ to 47° 38′ N.; includes Hand Rock, Carroll Islets, Bald Island, Jagged Islet [now Island] (Fig. 1C), Cake Rock, James Island, Huntington Rock, Quillayute Needles (Fig. 1D), Rounded Islet [now Round Island], Alexander Island, Perkins Reef, North Rock, Middle Rock, Abbey Island and South Rock.

3. Copalis Rock National Wildlife Refuge

   From 47° 29′ to 47° 08′ N.; includes Arch Island, Sea Lion Rock, Willoughby Rock, Split Rocks, Sonora Reef, Greenville [now Grenville] Arch (Fig. 2), and Copalis Rock.

Aerial surveys. — The first five aerial surveys were made by Kenyon in aircraft of the Sand Point Naval Air Station, Seattle, on 14 April 1949, 5 June 1950, 29 March 1951, 11 February 1953, and 11 May 1954. He counted marine mammals only. The sixth aerial survey was made on 13 July 1959 in a Grumman Albatross by courtesy of the U. S. Coast Guard as authorized

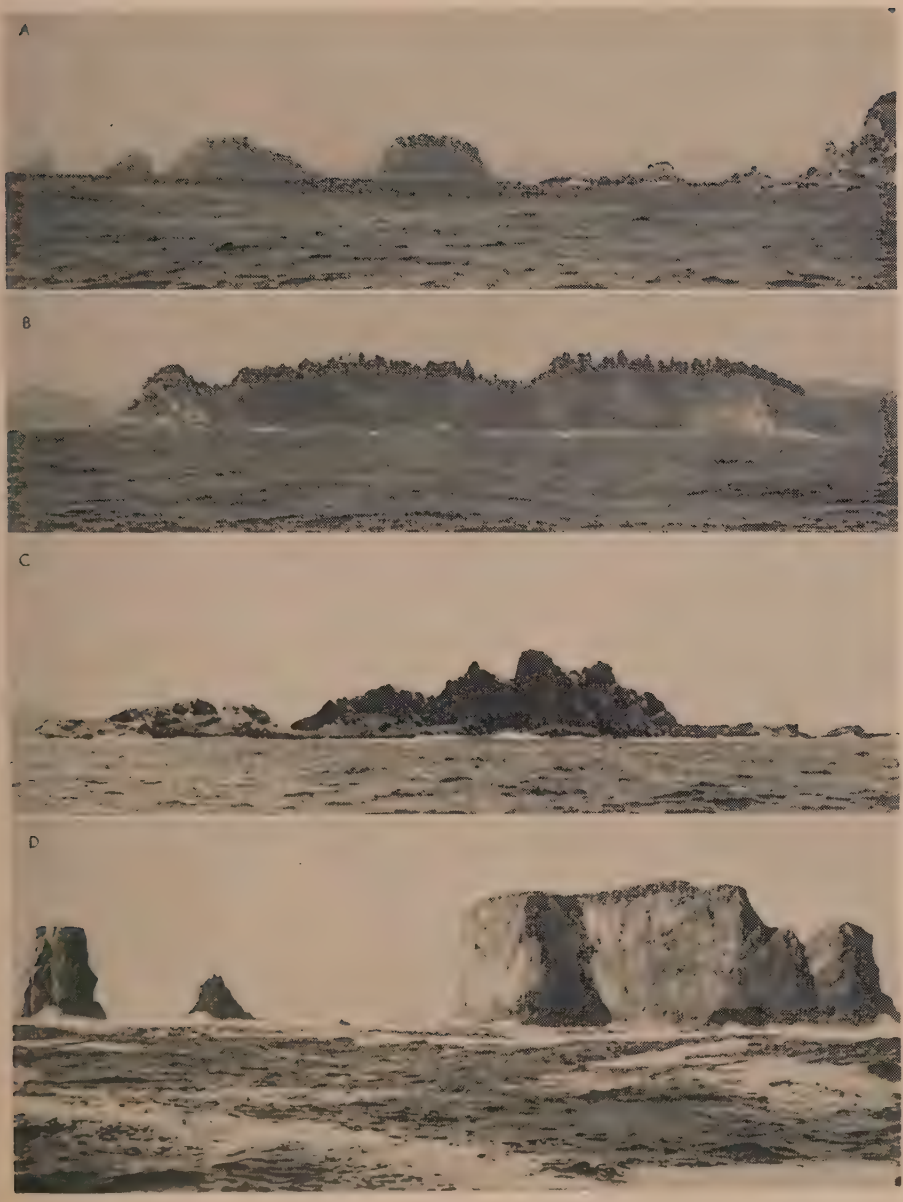

Figure 1—

A. Bodelteh Islets looking north, tip of Ozette Island at right. 17 July 1959. VBS 4258.

B. West side of Ozette Island. A family of Peregrine Falcons occupied cliffs at the southern end of the island. 17 July 1959. VBS 4261.

C. Jagged Island. A favorite hauling ground for sea lions. 25 July 1941. VBS 1205.

D. Quillayute Needles, near Lapush. 10 April 1941. VBS 1162.

by Rear Admiral Allen B. Winbeck. The plane was piloted by Commander J. N. Schraeder and Lt. (jg.) W. A. Calder. Observers were Kenyon and Scheffer with Garret Eddy (Pacific Northwest Bird and Mammal Society) and Frank Richardson (University of Washington). The party estimated the distribution and numbers of marine birds as well as mammals. All of the six aerial surveys were made at altitudes between 15 and 120 meters (50 and 400 feet) and at air speeds between 220 and 260 kilometers per hour (120 and 140 knots).

Surface survey. — After we had studied the reconnaissance photos taken on the 13 July 1959 flight, we visited the area by boat and on foot. The party included Kenyon, Scheffer, Eddy, Richardson, William Hawkins (student, University of Washington), and Robert Twist (U. S. Fish and Wildlife Service, Refuge Manager for the coastal series of National Wildlife Refuges between Puget Sound and northern California).

At 0500 on 15 July we left the Coast Guard station at Neah Bay in a 40-foot motor lifeboat. We cruised along shore from Waadah Island to Cape Flattery, to Waatch Point, across Mukkaw Bay, then due west into the open sea for 4 miles, then directly to Tatoosh Island. All pelagic birds seen (albatrosses and shearwaters) were more than 2 miles from shore. From 0800 to 1700 we inspected all of the larger rocks in the Tatoosh complex. Although Tatoosh Island has been occupied by man for many years, it appeared to be free of cats and rats at the time of our visit.

Figure 2.—Grenville Arch, photographed from the southeast. Cormorants (species?) nest on the summit of the larger rock and a few Glaucous-winged Gulls on the smaller. 13 July 1959. VBS 4289.

From 0730 to 1300 on 16 July we traveled by chartered troller from Neah Bay to Ozette Island. We saw approximately the same kinds and numbers of birds as on 15 July. From 1400 to 1800, on a circuit of the entire beach of Ozette Island, we saw deer tracks. Among the rocks we found a scat (from a raccoon or coyote?) containing feathers and crab shells. Some animal stole eggs from our camp during the night. Predators undoubtedly account for the dearth of nesting marine birds here.

At 0730 on 17 July we left Ozette Island in a dory with outboard motor and crossed 1 mile of open water, making a landing on the large cobblestones of the east island of the Bodelteh group. Kenyon and Scheffer surveyed all accessible coastline. Apparently predation is not serious, since the marine birds (glaucous-winged gulls, auklets, and petrels), appear to occupy all suitable habitat. A few tufted puffins nest near the tops of island cliffs. The lack of nesting murres was somewhat puzzling.

We suppose that precipitous rocks of the mainland coast are accessible to land predators, for we saw indications that only a few cormorants may nest here; we saw no other marine birds.

List of species. — Thirty-two species of marine birds, two raptorial birds, and six marine mammals are included in the following annotated list. Population estimates are given in the list and in the summary.

All dates are in 1959 unless otherwise noted.

Gavia immer. Common Loon. One seen off Cape Flattery on 15 July.

Diomedea nigripes. Black-footed Albatross. One seen about 4 miles offshore on 15 July.

Fulmarus glacialis. Fulmar. Two seen during the boat trip from Cape Flattery to Ozette Island on 16 July.

Puffinus creatopus. Pink-footed Shearwater. About 200 seen in flocks offshore, south of Tatoosh Island on 15 July; similar numbers between Cape Flattery and Ozette Island on 16 July.

Puffinus griseus. Sooty Shearwater. About 1,000 seen offshore south of Tatoosh Island on 15 July; similar numbers between Cape Flattery and Ozette Island on 16 July.

Oceanodroma furcata. Fork-tailed Petrel. None seen at sea; none found nesting on Tatoosh Island. Although remains of one were found among rocks on Ozette Island on 16 July, no petrels were seen or heard during a night watch for them. Richardson (1960) has already recorded our observations of petrels nesting on the Bodelteh Islets.

Oceanodroma leucorhoa. Leach's Petrel. Nesting burrows were numerous beneath lush vegetation on the north islet of the Tatoosh group and not uncommon on the southwestern islet. Adults and eggs were taken from several burrows on 15 July. Burrows, and birds nesting under rocks, were also numerous on the Bodelteh Islets. No nests or sign could be found on Ozette Island. Jewett *et al.* (1953, p. 75) cited population estimates of 100,000 for "the off-shore islands" of Washington and 19,00 to 21,000 for five of the islands in our survey area.

Phalacrocorax auritus. Double-crested Cormorant. Four seen on 15 July among the offshore rocks of Cape Flattery. This species and the next were not identified from the air.

Phalacrocorax penicillatus. Brandt's Cormorant. Ten to fifteen recorded at Tatoosh Island on 15 July.

Phalacrocorax pelagicus. Pelagic Cormorant. Among the rocks off Cape Flattery, 335 were counted during the boat survey on 15 July. During the 13 July aerial survey the following estimates were made: White Rock, 50; Cape Johnson Islets, 20; Cake Island and Bald Island, 50; Quillayute Needle, 25; Alexander Island, 10; North Rock, 50; Sea Lion Rock and Split Rock, 150; Grenville Arch, 25. Fifty-five nests occupied a cliff on the west side of Ozette Island. About 30 pairs of cormorants nested on cliff ledges of the Bodelteh Islets.

Branta nigricans. Black Brant. One seen on Mukkaw Bay on 15 July.

Anas acuta. Pintail. One seen near Cape Flattery on 15 July.

Histrionicus histrionicus Harlequin Duck. Two seen among rocks off Cape Flattery on 15 July; three foraging among rocks at Bodelteh Islets on 17 July.

Melanitta deglandi. White-winged Scoter. One seen off Cape Flattery on 15 July.

Melanitta perspicillata. Surf Scoter. Two seen off Cape Flattery on 15 July.

Haliaeetus leucocephalus. Bald Eagle. On 29 March 1951, three subadults were soaring near Quillayute Needle. From two to four adults were seen at different locations on each of the first five aerial surveys. Three adults were resting on cliffs and trees near the tip of Cape Flattery on 15 July and two were flying among the Bodelteh Islets on 17 July.

Falco peregrinus. Peregrine Falcon. Two adults and one subadult seen on the cliffs on the south side of Ozette Island on 16 July. The adults circled and called, perhaps indicating that this was their nesting area. Beebe (1960), noted that he found no sign of nesting along the Washington coast after 1958. Jewett *et al.* (1953, p. 186) stated that it "is a fairly common species on the off-shore islets from Flattery Rocks to Cape Disappointment." Skeletal remains of Fork-tailed Petrels found on one of the Bodelteh Islets, as noted by Richardson (1960), might have been dropped there by the pair of falcons we observed.

Haematopus bachmani. Black Oystercatcher. Thirty-one, singly or in small groups, were foraging among rocks along the shore of Cape Flattery on 15 July and an additional 15-20 were seen at Tatoosh Island. Fifteen were counted on a circuit of Ozette Island and 40, divided among three flocks, were seen on the Bodelteh Islets on 17 July and one nest containing four eggs was found here. Because of their small size and dark color, few oystercatchers were observed during aerial surveys.

Arenaria melanocephala. Black Turnstone. Six were seen on the Bodelteh Islets on 17 July.

Heteroscelus incanum. Wandering Tattler. Two individuals seen along the shore of Ozette Island on 16 July and four among the Bodelteh Islets on 17 July.

Phalaropus sp. Phalarope. About 100 were seen during the boat trip between Cape Flattery and Ozette Island on 16 July. They appeared to be *P. fulicarius,* but all were at a considerable distance and not positively identified.

Larus glaucescens. Glaucous-winged Gull. The most numerous bird observed; estimated numbers: Cape Flattery area, 400; Tatoosh Island, 2,000 (nesting); Umatilla Reef and Bodelteh Islets, 2,500 (nesting); White Rock,

100; Cake Island and Bald Island, 200; Quillayute Needle, 500; Giants' Graveyard, 25 Alexander Island, 25; Sea Lion Rock and Split Rock, 1,500; Grenville Arch, 600. At two large breeding colonies on Tatoosh and Bodelteh Islets, 15 and 17 July, eggs were hatching, and young up to a week or more old were hiding in the grass. Several nests were found on the pinnacle on the western side of Ozette Island but only one contained eggs. Jewett *et al.* (1953, p. 293) estimated the population on the west coast islets at 10,000; a figure close to our estimate of 10,000 to 15,000.

Larus occidentalis. Western Gull. Three seen at Tatoosh Island, 15 July.

Larus californicus. California Gull. Four seen at Ozette Island on 17 July.

Larus philadelphia. Bonaparte's Gull. Ten seen near Ozette Island on 17 July.

Larus canus. Mew Gull. Two seen during the boat trip from Cape Flattery to Ozette Island on 16 July.

Larus heermanni. Heerman's Gull. Several flocks, totaling 670 birds, were searching for food or resting on rocks along the Cape Flattery coast on 15 July. Several more seen at Tatoosh Island on 15 July and about 40 at Ozette Island on 16 July.

Rissa tridactyla. Black-legged Kittiwake. Off Cape Flattery, small flocks and individuals totaling 52 birds were resting on rocks and feeding; an additional 50 seen near Tatoosh Island on 15 July. The majority were in immature plumage.

Uria aalge. Common Murre. About 200 pairs were nesting on cliffs at Tatoosh Island and 550 birds were recorded during the boat survey off Cape Flattery. Estimates obtained during the aerial survey on 13 July were: Umatilla Reef and Bodelteh Islets, 100; White Rock, 100; Cake Island and Bald Island, 50; colonies of about 2,000 murres were seen on two islets, probably Carrol Island and Willoughby Rock (at this point in the flight we were uncertain of exact locations). None was nesting on Ozette Island, and we found none nesting on the Bodelteh Islets. Only the two large colonies noted above were seen.

Cepphus columba. Pigeon Guillemot. Because of their small size and dark color only a few could be seen from the air and no record of numbers was kept. On the surface surveys, 15-17 July, 4 were seen near Cape Flattery, approximately 15 on rocks along the shore at Tatoosh Island, and 6 at the Bodelteh Islets.

Brachyramphus marmoratum. Marbled Murrelet. Four seen during the boat trip from Cape Flattery to Ozette Island on 16 July.

Ptychoramphus aleutica. Cassin's Auklet. Scattered individuals totaling 365 were seen on the 15 July boat survey. Many were nesting on the Bodelteh Islets on 17 July. On Ozette Island on 16 July we found a few feathers among rocks on the hillside but no nests.

Cerorhinca monocerata. Rhinoceros Auklet. Nine seen on 15 July around Cape Flattery and Tatoosh Island, but no nests on any of the islands surveyed. Richardson (letter) believes that several thousand breed on Destruction Island.

Lunda cirrhata. Tufted Puffin. Off Cape Flattery on 15 July, 65 seen. An estimated 25 pairs were breeding on Tatoosh Island and 10 pairs on the Bodelteh Islets. During the aerial survey on 13 July, a rough estimate of birds was recorded: Umatilla Reef, 20; White Rock, 10; Cake Island and

Bald Island, 30; Quillayute Needles, 25; Sea Lion Rock and Split Rock, 50; Grenville Arch, 50. Many others were seen in the water. Dawson (*In* Jewett *et al.*, 1953, p. 332) estimated the population on Carroll Island alone at 5,000 to 10,000. Quite possibly oil pollution on the sea in recent years has cut the population. On the other hand, this dark-bodied bird is not easily seen from the air, and our estimate may be low.

Eumetopias jubata. Steller Sea Lion. In manuscript reports of George G. Cantwell describing his visits to Jagged Island each summer from 1914 to 1917, we find casual mention of large numbers of sea lions: "On Jagged Island (10 August 1916) . . . the big sea lion herd here in full force, between 2,000 and 3,000 of the huge animals were sunning themselves about the rock."

There is no record that the Steller sea lion has *bred* in historical times on the islets or along the coast of Washington. All observations indicate that it does not, and that the local population does not now, at any season, exceed about 500. Jagged Island and Split Rock appear to be favorite winter hauling grounds; Spike Rock and Umatilla Reef midsummer grounds. Because little has been written about sea lions in Washington, we give the following estimates in detail:

Date	*No. Seen*	*Location*	*Remarks*
14 April 1949	50-75	Jagged Island	Bulls in the majority
14 April 1949	40	Split Rock	Adults and subadults
5 June 1950	55	Split Rock	4 or 5 large bulls; subadults, several adult females (?); no pups.
29 March 1951	120-150	Jagged Island	Adults and subadults
29 March 1951	75-100	Split Rock	Adults and subadults
11 Feb. 1953	200	Jagged Island	Adults and subadults
11 May 1954	50	Jagged Island	10-15 adult males
13 July 1959	20	Spike Rock area	Mostly Subadults, no pups
13 July 1959	250	Umatilla Reef	Mostly Subadults, no pups
13 July 1959	100	Jagged Island	Mostly Subadults, no pups
13 July 1959	5	Split Rock	Mostly Subadults, no pups
15 July 1959	2	Cape Flattery	Subadult males

Zalophus californianus. California Sea Lion. On 5 June 1950, two sea lions among about 55 *Eumetopias* on Split Rock appeared to be *Zalophus.* They plunged into the water, however, before a second pass was made over the islet. On 11 May 1954, two adult male *Zalophus* were observed from low altitude flight among the *Eumetopias* on Jagged Island.

At least a few adult male California sea lions move northward regularly in winter months as far as Sea Lion Caves near Florence, Oregon (Kenyon saw 34 there on 14 December 1951 and 21 on 11 March 1958). No specimen records are available for the Washington Coast. The observations recorded above, as well as skeletal remains recorded from the outer coast of Vancouver Island, British Columbia (Cowan and Guiguet, 1956) indicate that *Zalophus* may occasionally venture into Washington waters.

Phoca vitulina. Harbor Seal. Dark-colored animals hauled out on kelp-covered rocks were not easily seen from the air. Ten seals were seen at the Giants' Graveyard and two at Alexander Island during the aerial survey of 13 July. Only one was seen near Cape Flattery on the 15 July surface

survey. A dead one (shot?) was floating in a kelp bed near an anchorage used by fishing boats at Ozette Island. Because harbor seals haul out irregularly, and are difficult to see, such surveys as ours reveal an unknown fraction of the numbers present. Even so, we saw fewer than we had expected. Bays along the Washington coast south of the survey area, perhaps offering more attractive habitat, support populations numbering in the hundreds.

Phocoena phocoena. Harbor Porpoise. Five seen off Cape Flattery on 15 July; none seen during aerial surveys.

Balaenoptera acutorostrata. Little Piked Whale. Two seen off Cape Flattery on the 15 July boat survey; none recorded during aerial surveys.

Megaptera novaeangliae. Humpbacked Whale. On 14 April 1949, the weather was calm and clear. Forty to fifty whales were seen between Tatoosh Island and Copalis, where the survey was discontinued. They were between 1.5 and 3 km from shore. The majority were loafing near the surface. Several groups of two and three were lolling just below the surface, their snouts nearly touching and their flukes sagging, so that they lay at an angle of about 30° to the surface. Two were rolling about side-by-side, waving their long fore flippers in the air.

On 5 June 1950, the weather was calm and clear. On a survey from Cape Alava to Cape Shoalwater, two whales were seen loafing near the surface about 1.5 km off Cape Alava and two more about 1.5 km south of Jagged Island near the 10 fathom curve.

On 29 March 1951, the weather was clear, with a light westerly breeze. On a survey from Quillayute to Grays Harbor, one whale seen about 8 km north of Destruction Island and 3 km from the coast.

On 11 February 1953, there was a high overcast, with westerly wind 15 to 20 knots. On a survey from Cape Flattery to Grays Harbor no whales were seen.

On 11 May 1954, the sky was overcast, with rain squalls and a southwesterly breeze. On a survey from Tatoosh Island to Grays Harbor, two whales were seen off the mouth of the Quillayute River: an adult about 1.5 km offshore and a subadult about 0.2 km offshore.

On 13-17 July, during our aerial and surface surveys, no whales were seen. Our observations indicate that migrating whales pass along the Washington coast in greatest numbers in April and are scarce or absent near shore at other times.

Summary and discussion. — A recapitulation of counts and estimates of certain birds and marine mammals is given below. The estimated total population is also given.

BREEDING MARINE BIRDS

Species	*Field count or estimate*	*Estimate of total population*
Fork-tailed Petrel	Numerous, nesting in certain areas	
Leach's Petrel	Numerous, nesting in certain areas	
Double-crested Cormorant	4	100-200
Brandt's Cormorant	15	100-200
Pelagic Cormorant	905	1,500-2,500
Black Oystercatcher	100	300-600
Glaucous-winged Gull	7,850	10,000-15,000
Common Murre	5,400	6,000-10,000

Pigeon Guillemot	25	200-500
Cassin's Auklet	365	Several thousand
Rhinoceros Auklet	9	?
Tufted Puffin	320	1,000-2,000

MARINE MAMMALS

Steller Sea Lion	377	400-500
California Sea Lion	2	Scarce
Harbor Seal	13	100-200
Harbor Porpoise	5	?
Little Piked Whale	2	?
Humpbacked Whale	40-50	Several hundred, spring only

Several unconfirmed reports of sea otter *(Enhydra lutris)* in the area have been received by the Fish and Wildlife Service. Prior to its extermination on the Washington coast in the early 1900's, it had been abundant off the Olympic Peninsula (Scheffer, 1940). Because sea otters might wander to the Washington coast from California or Alaska population reservoirs, particular effort was made during our surveys to find them. Though many areas appear to offer ideal habitat, no sea otters were seen.

Although we have seen no California Gray Whale *(Eschrichtius gibbosus)*, we are told that there are numbers near Lapush annually, February to June. Certainly they are regular migrants along this coast.

At the time of our survey, the three National Wildlife Refuges we visited were not posted. We saw two fishermen with guns landing on Ozette Island on 16 July. Steps are now being taken, in view of increasing interest in wildlife and wilderness areas, to post the islands and to publicize their status on U. S. Coast and Geodetic Survey charts. During the nesting season, great damage could be done by casual and thoughtless visitors.

—U. S. Fish and Wildlife Service

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SURING THE PRODUCTION OF MARINE PHYTO-ANKTON. *By J. D. H. Strickland. (Fisheries Research Board of Canada, Bulletin No. 122). The ueen's Printer, Ottawa. 1960. 172 pp., 9 tables. .00.*

ne author states that there is "no comprehensive critical review of marine primary productivity serves as an adequate introduction to the sub- in all its aspects for workers about to commence e research in this field." In this publication the or attempts to satisfy this need by presenting in r, concise language an excellent introduction to measurement of primary productivity of marine oplankton. Not only is he successful in provid- a valuable text for new workers, but also he s questions which might profitably be further mined by researchers already in the field.

ne publication is divided into five sections. A e of contents, a glossary of symbols and abbrevi- ns, introductory remarks, and an extensive bibli- phy are also included.

any introductory text an author is confronted the problem of using terms, which although fa- ar to the experienced worker, are unknown to neophyte. The author, realizing this, has devoted entire section to a compact, yet thorough, discus- of definitions and conversion factors.

a discussion of the chemical composition of oplankton in Section II the author adequately ers the elementary composition, the major molec- constituents, and the pigments used in measur- primary productivity. Briefly covered in each ance is a review of the literature, the relationship ween constituents, the degree of variations in surements and their causes, and the limitations alues determined for each constituent as used in orting the findings. Possible solutions for some he problems which arise when measuring chem- composition of phytoplankton are given, and eral techniques with their limitations used for ob- ing these measurements are introduced.

he primary problem of measuring a standing crop organisms is to obtain a representative sample of opulation which is distributed unevenly over an ensive area. In Section III the author covers the blem of gear selection, of processing the sample, l of separating phytoplankton from all organic ter of animal origin and detritus. This is fol- ed by a discussion of the techniques employed in mating primary productivity from carbon content, ogen, phosphorus, and specific organic constitu- , and by pigment analysis. Discussing each se separately, the author provides a brief review the literature succeeded by a discussion of the tations. This section is terminated with a dis- ion of some results of standing crop determina- obtained by various workers.

ection IV, a discussion of the measurement of the of photosynthesis, is by far the best portion of text. Introducing this topic, the author provides informative discussion of oxygen and carbon di- e requirements and relationships, photosynthetic respiratory quotients, effects of illumination on piratory algae, and participation of intracellular erial and the interpretation of radiocarbon pro- tivity measurements. The problem of sampling direct measurements is discussed again, and al- though slightly repetitious of Section III, this additional coverage is beneficial to the neophyte in that it provides further insight into the problems encountered in the field and laboratory. Having presented this background information, the author then covers the measurement of the rate of photosynthesis by carbon dioxide consumption, the oxygen evaluation (dark and light bottle), the rate of carbon-14 uptake, methods based on pigment content, and finally by other methods which involve depth profiles of oxygen or phosphorus concentrations and the uptake of phosphorus. In each instance he provides a brief review of the literature, general techniques, limitations, and special considerations to be taken into account. Terminating the discussion of measuring the rate of photosynthesis, the author provides a table and brief discussion of selected examples of productivity measurements.

Section V is "a detailed discussion of the measurement of primary productivity in nature and of methods designed to predict *in situ* productivity with the minimum amount of experimentation." Before delving into this subject, the author provides a brief discussion of the concept of the productivity index of a water mass. Then, in a discussion of general kinetics, the author covers the kinetics of unicellular growth and decay, the influence of light, and the diurnal fluctuation of organisms as related to timing of experiment. Concluding the text, productivity measurement in nature is presented with the author providing additional observations on population changes in nature and the *in situ* production and its prediction from experimental work using light incubators.

Mr. Strickland has shown that he is well acquainted with his field, and the direct, clear manner in which the material is presented is to be commended. The reference section, although not covering the entire field, is an adequate introduction to the beginner as well as a usful tool to the experienced worker.

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RATE OF METABOLISM AND FOOD REQUIREMENTS OF FISHES. *By G. G. Winberg. (Fisheries Research Board of Canada, Translation Series No. 194). (Published in Nauchnye Trudy Belorusskovo Gosudarstvennovo Universiteta imeni V. I. Lenina, Minsk, 253 pp., 1956). Fisheries Research Board of Canada, Biological Station, Nanaimo, B. C. 1960. 202 pp., 54 figs., 32 tables.*

This translation of G. G. Winberg's monograph represents a cooperative enterprise of the Fisheries Research Board of Canada, the Department of Zoology of the University of Toronto, and the Research Division of the Ontario Department of Lands and Forests.

Much of the monograph is devoted to reviewing the various relationships of the metabolic rate of fish to factors such as temperature, the oxygen content of water, total body size and weight, salinity, diurnal fluctuations in metabolism, and differences between species. In this discussion he is concerned

only with measurements of the *rate* of metabolism. Physiological and biochemical mechanisms of fish metabolism, although acknowledged to be important, are not considered.

During the discussion of metabolic rate and total body size, considerable effort is expended in showing that the relation of metabolism to size can be expressed by a parabolic equation, *i.e.*, $Q = Aw^k$, where Q is the rate of oxygen consumption, A is a coefficient equal to the total metabolism of an amount of unit weight, w is the weight of the animal, and k is a constant indicating at what speed and in which direction the metabolic rate changes when weight increases. In explaining this relationship he has attempted to use all of the published results of measurements of fish metabolic notes. Not every measurement examined was included in the analysis, however, as only those data accompanied by weight and in a form that could be adjusted to milliliters of oxygen consumed per gram of weight per hour at 20 degrees Centigrade could be used.

These data are grouped according to related species in 13 tables, including for each observation the name of the fish, the author and year of publication of the source paper, the method of determination used by the author, the number of determinations, the average temperatures at which measurements were obtained, and the average value of the rate of metabolism expressed in the units used in the original paper. The result is 369 pairs of weight and metabolic rate data. However, for various reasons certain data on single measurements of very tiny fish were excluded. For the remaining 364 pairs of values Winberg obtains: $k = 0.815 \pm 0.0105$. He expresses as a first approximation, the general relationship between the mean value of total metabolism and weight by the equation, $Q = 0.3\, w^{0.8}$. This equation is basic to the understanding of much of the remainder of the monograph.

Brief comparisons of metabolic rates of crustaceans and warm-blooded vertebrates with fishes are also made.

A discussion of differences in the metabolic rates of ecological groups is included. In a portion of this commentary Winberg states, as a hard, incontrovertable fact, that the question of differences in the relative metabolic rate of marine and fresh-water fishes can be regarded as solved since he shows the average metabolism is the same for the two groups. This may well be so, but the evidence is certainly empirical and does not warrant such dogmatism. For instance, he shows that k for marine fish is equal to 0.79 ± 0.014, while for fresh-water fish it is 0.81 ± 0.014. The differences, though small, are nonetheless differences, and their very existence does not support his attitude of finality. This criticism by the reviewer must appear to the reader as an instance of making a "mountain of a mole hill," but at this point in the monograph the uncompromising and dogmatic style of the author begins to obtrude on the sensibilities.

A discussion of active metabolism and energy expenditures of fish in motion is included and points up the present lack of knowledge and the necessity for more and careful work on this aspect of fish metabolism.

The balance of the monograph is concerned with the food requirements portion of the title and the dynamics of the growth and metabolism of fish. The interrelationship of growth, food, and metabolic rate are considered, and computation methods for determining such things as the rate of increase in weight and the food intake of fish are developed.

In these areas the author apparently feels more confident, and even when he disagrees with a source his criticism is less acrid.

The review of literature alone is valuable because of its highly critical but often polemic discussion of Russian work in the field of fish metabolism through 1954. Approximately 90 Russian papers are cited, of which not more than 10 have been used in English reviews available to me. I use the term "approximate" because text citations do not always appear in the list of references. He has not limited himself to Russian workers alone but also includes 136 non-Russian papers.

The compilation of data in the numerous tables of the monograph will prove to be the most useful compendium of information on the metabolic rate and food requirements of fish now available. In addition to the 13 composite tables of measurements of rate of oxygen consumption for such diverse species groups as minnows, sturgeons, and lampreys, there is a series of 7 tables of growth rate, food consumption, and metabolic rate for various species.

The air of personal infallibility displayed by Professor Winberg in dealing with data and authors who do not agree with him, adds neither dignity nor stature to his position as a scientist.

Despite his dialectic shortcomings, Professor Winberg has contributed a useful and important monograph on the subject and implications of the metabolic rate of fishes.

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Recent Publications

Alexander, Elizabeth C.

A Contribution to the Life History, Biology and Geographical Distribution of the Bonefish, *Albula vulpes* (Linnaeus). *(Dana Report No. 53). Carlsberg Foundation, Copenhagen. 1961. 51 pp. 15. Danish Kr.*

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Recent Sediments, Northwest Gulf of Mexico. *A symposium summarizing the results of work carried on in Project 51 of the American Petroleum Institute, 1951–1958. Edited by Francis P. Shepard, and others. Tulsa, Oklahoma. 1960. 394 pp. $7.00.*

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Recent Trends in White Shrimp Stocks of the Northern Gulf[1]

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Abstract

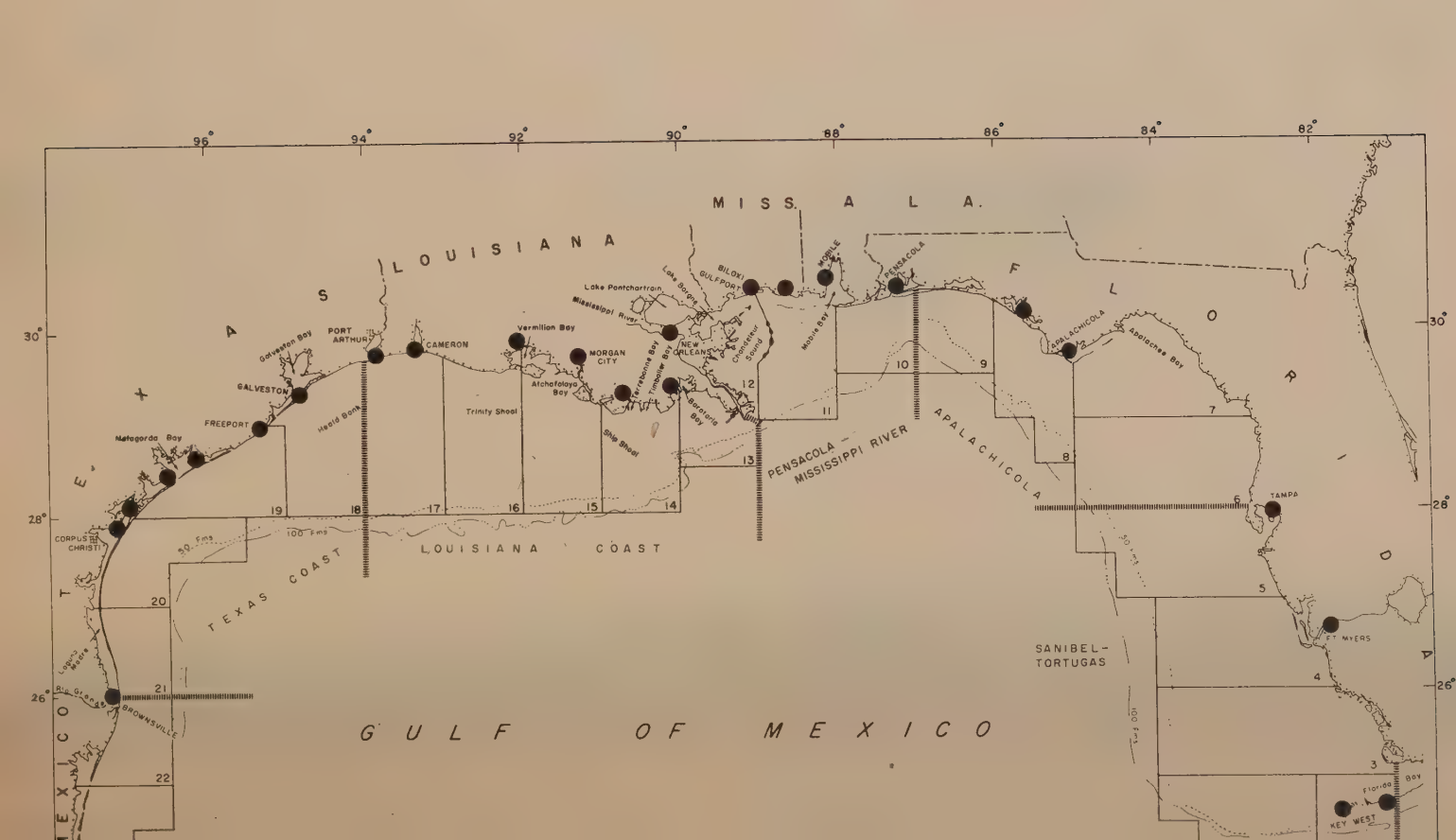
Fishery statistics compiled since 1956 by the Bureau of Commercial Fisheries are used to determine seasonal and long-term trends in the abundance of white shrimp along the northern Gulf coast. Special reference is made to that portion of the coastal stocks contributing most to this species' over-all commercial production, namely, that portion inhabiting Louisiana's marshes and offshore waters. By providing some insight into population age structure, commercial size composition data aid in hypothesizing causes of the sharp production drop in 1957.

HISTORICALLY THE MAINSTAY of one of the Nation's major fisheries, the white or common shrimp, *Penaeus setiferus*, no longer holds the spotlight. During the past 2 decades, which have seen a great expansion in the industry utilizing the Gulf of Mexico's shrimp resources, this species has become increasingly subordinate in importance to two related forms, *viz.*, the brown and pink shrimp, *P. aztecus* and *P. duorarum* respectively. This is not to say, however, that the condition of its stocks now merits only passing attention for in some coastal areas and at certain seasons the white shrimp still represents the cornerstone of local economy.

Recent statistics disclose that the white shrimp contributes roughly 25 per cent to the annual production of all shrimps in the United States Gulf coast area. Over the period 1956-1960, commercial landings originating in northern Gulf waters ranged from a low of 18.6 million pounds (1957) to a high of 47.0 million (1960). Their dockside value within the same period rose from a corresponding low of 6.9 million dollars in 1957 to 14.8 million the following year. Note here that the ratio between quantity and value of landings is not necessarily constant but fluctuates according to economic conditions within and without the industry.

Because of its former (apparent) dominance and related significance as a fishery product, much more attention has been given the biology and dynamics of the white shrimp than has been accorded the other commercial varieties. But, despite advances made, large gaps still exist in our knowledge of what factors, natural and artificial, exercise the greatest control over the magnitude of commercial shrimp stocks — be they brown, pink, or white. Determination

[1]Contribution No. 149 of the Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas.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Lake Pontchartrain
Mississippi River
NEW ORLEANS
Chandeleur Sound
Mobile Bay
Galveston Bay
PORT ARTHUR
CAMERON
Vermilion Bay
MORGAN CITY
Terrebonne Bay
Timbalier Bay
Atchafalaya Bay
Barataria Bay
GALVESTON
FREEPORT
Matagorda Bay
Heald Bank
Trinity Shoal
Ship Shoal
PENSACOLA – MISSISSIPPI RIVER
APALACHICOLA
TAMPA
FT MYERS
CORPUS CHRISTI
BROWNSVILLE
Laguna Madre
Rio Grande
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of these factors and of how they operate to cause adverse fluctuations in supply, persists as a major objective of shrimp research.

Acknowledging the usefulness of commercial fishery statistics in achieving such an objective, the Bureau of Commercial Fisheries initiated a Gulfwide industry canvass in 1956. It has since functioned continuously, gathering and compiling a wealth of detailed information which includes statistics of fishing operations, shrimp production, and landings' composition (species and size). Published tabulations thereof provided the data used throughout this report. Insofar as these data permit, recent trends in the relative strength of a major portion of the northern Gulf's white shrimp stocks are described, and an explanation for one instance of an untoward drop in yield is attempted.

White Shrimp Biology and Distribution

A considerable literature dealing with the taxonomy, morphology, general biology, and ecology of the white shrimp has accumulated over the past 30 or so years. For an introduction to detailed information on these subjects one should consult the general works of Burkenroad (1934, 1939); Pearson (1939); Young (1959); and Lindner and Anderson (1956). Suffice it to say here that the white shrimp is one of perhaps a dozen and a half Gulf of Mexico Penaeidae, a family of shrimps having world-wide distribution but occurring mainly in tropical and subtropical zones. Its life history is characterized by an egg and larval phase in the open sea, a postlarval and juvenile phase in inshore brackish waters, and an adult (reproductive) phase, again, in the open sea. Off the United States Gulf coast, the reproductive season extends over the greater part of each calendar year with heightened activity evident at the beginning (spring) and toward the end (fall).

In the Gulf of Mexico, white shrimp are found in widely varying quantity on the continental shelf from the vicinity of Apalachicola (Florida) westward along the coast and then south to the Bay of Campeche (Figure 1). Densest concentrations seem to prevail in the more humid regions where a low-lying coastline consists of a series of broad estuarine systems. One such region harboring a sizable population is the east-Mexican coastal area between Tupilco and Carmen. But by far the more important is that section of the United States coast stretching from Apalachicola to central Texas. Within it, specifically in and seaward from Louisiana's vast estuarine complex, white shrimp stocks attain peak strength. Although the preponderance of stocks at all coastal points lies within the 15-fathom contour, the deeper limit of the species bathymetric range is in the neighborhood of 40 fathoms.

Manner and Intensity of Fishing

All penaeid shrimps, being bottom dwellers during all but their earliest life history stages, are readily captured with bottom trawls of any type. Otter trawls of varying dimensions are, however, the conventional gear employed by the Gulf shrimp fleet. Contrasted to the earlier practice of fishing one large (60- to 110-foot) "flat" or "balloon" net, current procedure in the case of most vessels plying offshore waters consists of fishing a pair of smaller (40- to 50-foot) nets. Small craft restricted to inshore waters have the capacity

FIGURE 1. System for coding origin of shrimp landings and position of commercial shrimping operations in the northern Gulf of Mexico. Shaded circles indicate principal landing ports.

FIGURE 2. Distribution of commercial shrimp fishing effort on the continen shelf of the northern Gulf of Mexico (statistical subareas 7-21), 1956-19

to pull but a single net, the width of which ordinarily does not exceed feet or is fixed at a lesser dimension by state law. In all fleet componer mesh size (stretched) varies little from 2¼ inches. More detailed descripti of shrimp fishing gear and gear operation may be found in Knake et al. (195 Robas (1959), and U.S. Fish and Wildlife Service (1958).

White shrimp are ordinarily fished during daylight hours, this pointing a difference in habits which makes the brown and pink species more vulnera to capture during hours of darkness. Most fishing trips in northern G waters are of a day's duration, measured from departure to first landi Trips exceeding 5 calendar days are comparatively rare. Depending on seasonal occurrence of the various species, trawling may be done only night, only during hours of daylight, or around-the-clock. There has been recent evidence, in situations where two or three of the common variet overlap in occurrence, of the industry having special preference for a p ticular species and directing fishing effort accordingly. The price differen between species being negligible, major considerations are abundance, cessibility, and size.

To enhance their usefulness, statistics of fishing operations and production are reported systematically on the basis of coastal areas and depth zones into which the fishing grounds are subdivided (Figure 1). Intensity of shrimp fishing on the northern Gulf's continental shelf, as disclosed by effort statistics so reported, is shown diagrammatically for the period 1956-1960 in Figure 2. Note that season after season, certain well-defined areas receive the brunt of the total effort expended. More important, however, observe that some trawling is done the year round in nearly every coastal subsubarea. Knowledge of how fishing effort is distributed with respect to the known range of exploited stocks greatly aids the derivation of meaningful indices to each species abundance. In the case of the white shrimp, it is readily apparent that hardly a portion of its stocks escapes the trawl. In fact, one might facetiously ask if this species stocks couldn't be "sampled" less heavily and still obtain reasonably good measures of their relative size. There is little doubt that the grounds included in Gulf statistical subareas 13 through 21, inshore to 20 fathoms, comprise one of the world's heaviest fished areas.

Commercial White Shrimp Yield

Analytical treatment of extensive fishery statistics is often facilitated by grouping them on the basis of small geographical units. This was deemed necessary in the case of upper Gulf shrimp fishery statistics and four sections were consequently delineated. From east to west they are: the Apalachicola area (statistical subareas 6-10); the Pensacola-Mississippi River area (subareas 11-12); the Louisiana Coast area (subareas 13-17); and the Texas Coast area (subareas 18-21) (see Figure 1).

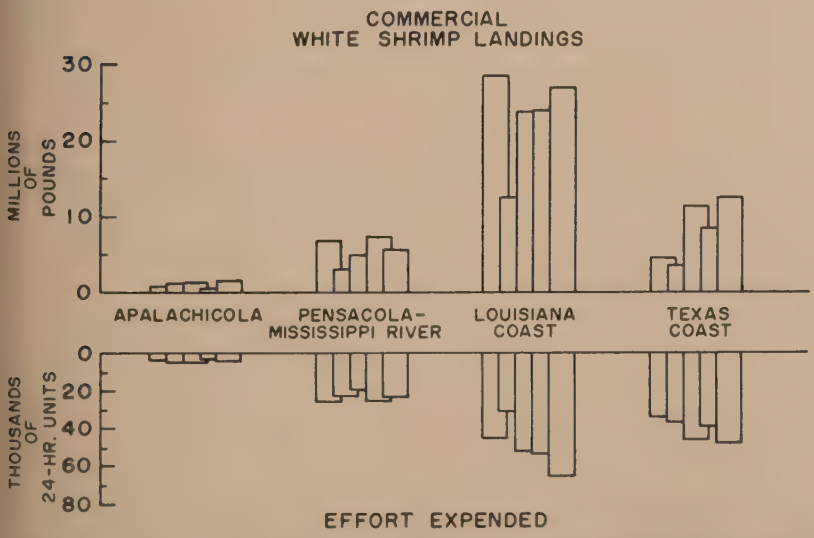


FIGURE 3. Annual white shrimp production and corresponding fishing effort in the northern Gulf coast area. Data for the years 1956-1960 are shown consecutively (left to right) for each coastal section.

Comparing the annual yield patterns in each coastal section, one merel concludes what was stated earlier, namely, that waters in the Louisiana are harbor the greater part of Gulf of Mexico white shrimp stocks (Figure 3 For this reason (as well as that of space limitations) the following discussio will be restricted to a treatment of statistics arising from fishing operation in the Louisiana Coast area, the thought being that trends, etc., elicited there from would largely reflect those of the coastal stocks as a whole.

Of the total shrimp produced commercially in this area, the white shrim makes up about 40 per cent. Over the years 1956-1960, its annual landing averaged 60 per cent of upper Gulf totals, ranging from a low of 10.5 millio pounds in 1957 to a high of 28.7 million the previous year (Figure 4A Ex-vessel values for the same years were 4.5 million and 8.3 million dollar On the average, inshore catches accounted for roughly 40 per cent of th area's annual white shrimp harvest, and consisted of 70, 28, and 2 per cen small, medium, and large shrimp[2] respectively. In contrast, relative compos tion of offshore landings was 25, 40, and 45 per cent in the same categorie As is well known, practically all of the small and much of the medium siz shrimp is marketed canned or dried, whereas the larger sizes are distribute fresh or frozen.

Seasonally, white shrimp landings in the Louisiana Coast area (as alon the northern Gulf coast generally) peak in November, with the bulk of eac year's harvest accumulating over the last 3 months of the calendar yea (Figure 4A). After the peaks are reached, yields of inshore population phase usually drop off more abruptly than do those of offshore phases. Yearly trend in annual offshore and inshore production exhibited a sharp drop in 195 followed, in the case of offshore production, by a slight rise during the perio 1958-1960, and in the case of inshore production, by nothing more than slightly undulating pattern over the same period. The over-all drop in 195 was of very great concern (Viosca, 1958) and culminated a gradual declin in white shrimp production which began soon after landings peaked in 194 at well over 110 million pounds.[3]

The cause or causes of the long-term reduction in white shrimp supplie will probably never be defined because of the lack of appropriate biologic and environmental measurements with which to formulate hypotheses, l alone test them. On the other hand, recent data at least offer some assistanc in speculating as to what brought about the 1957 situation.

Population Trends

The fished portion or exploited phase of a shrimp population shall be define as that fraction of the total population or stock whose lower limit is fixe either by the specifications of the gear (mesh size) most commonly employe by the fishing fleet, or by the minimum size of shrimp that will or can b accepted by processors. Since all statistics of commercial shrimp yield a reported in terms of weight, the foregoing connotation (stock) is furth modified to "fishable biomass." It is clear that commercial fishery statisti can only provide information about a population's fished or exploited phas

[2]Small shrimp are defined as those of uniform weight such that the numbers of whc individuals per pound would exceed 40, large shrimp as those that would number 15 or les
[3]Information taken from "Fishery Statistics of the United States—1956," Statistical Dige No. 43, U.S. Fish and Wildlife Service, 1958. Since large-scale exploitation of the brov shrimp was not yet underway, practically all of this production is assumed to ha consisted of white shrimp.

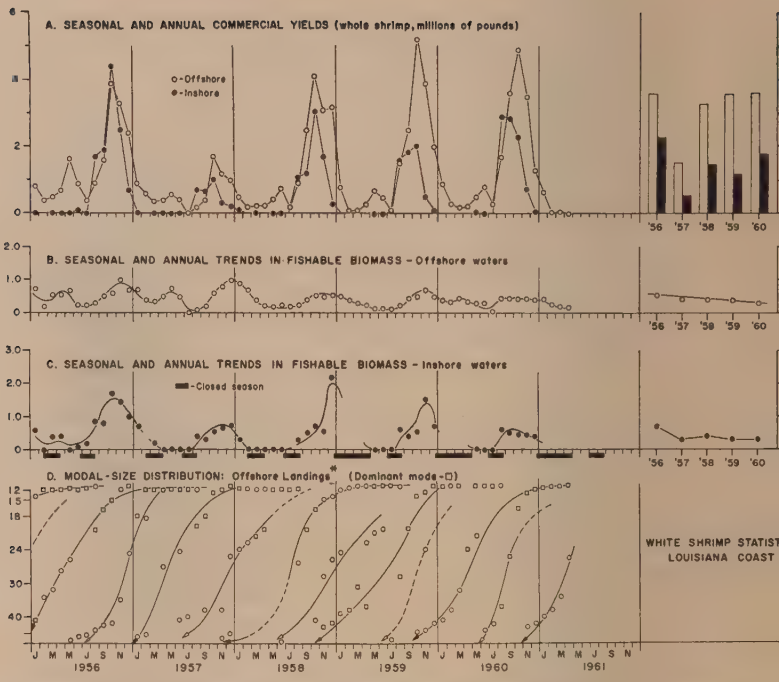
For a short interval of time, in this case 1 month, a catch (in weight)-effort ratio is computed for each subsubarea within the species range (*re* Figure 2). A weighted average ratio for all subsubareas is then determined, the sizes of each of these units constituting the weighting factors (Gulland, 1955). This ratio, the mean catch per unit fishing intensity, is theoretically proportional to the population's harvestable fraction and is referred to herein as a fishable biomass index. In effect, it is a density estimator in which the effects of uneven distribution of fishing effort are eliminated by a process analogous to stratified sampling. Note also that it yields indices having comparability in successive time increments. Thus a change in apparent density suggested by a difference in successive values of the simple catch-effort ratio could be wholly due to a change in effort distribution rather than a real change in population density. Employing the mean ratio of catch to fishing intensity circumvents this possibility.

Among the assumptions being made here, the following should be especially noted: (1) any white shrimp otherwise vulnerable but not available because of untrawlable bottom comprised a constant fraction of this species fishable biomass; (2) movement of commercial-size white shrimp into and out of the Louisiana Coast area was negligible or offsetting; and (3) characteristics of inshore and offshore fishing fleets (including gear specifications) changed little or not at all during the period of study.

Monthly (1956-1960) indices of fishable white shrimp biomass in the Louisiana Coast area are plotted serially in Figures 4B (offshore waters) and 4C (inshore waters). In each case there were generated typical time-series possessing distinct seasonal oscillations which obviously reflect to a great extent the species reproductive rhythm. No attempt was made to fit trend-curves by means of high order polynomials or other sophisticated statistical techniques, the feeling being that smooth curves fitted by eye would more than satisfy the purposes of this study. Indeed, the absence of numerous points would have, in the case of data plotted in Figure 4C, precluded the former approach anyway.

Though seasonal or cyclic oscillation is by far the dominant component in each time-series, the trend component is still discernible, albeit almost imperceptibly so. By plotting the monthly average indexes for each of the 5 years represented, seasonal effects were eliminated and the long-term components more clearly shown (right hand side of Figures 4B and 4C). In both offshore and inshore populations, these could be adequately described by straight lines, each characterized by a slight but yet distinctly negative slope. A straight line was, in fact, fitted to the monthly indices in Figure 4B. Unsystematic or "random" residual was almost negligible in both instances.

Having determined that the mean white shrimp biomass declined over the 5-year study period — nearly proportionately so in successive years — the problem remains to specify whether this actually signified a trend in the true sense of the word or merely part of another oscillatory component with mean period greater than that of seasonality. Regardless, determination of the causal systems underlying either of such conditions is a major objective of shrimp research. The most promising approach thereto involves the technique of serial or lag correlation. Here, the time-series of interest is correlated with a time-series of a factor which, on intuitive grounds, exercises some degree of control over it, and whose values lag a specified interval of time behind those of the former. To illustrate in the case of shrimp population research, one


A. SEASONAL AND ANNUAL COMMERCIAL YIELDS (whole shrimp, millions of pounds)
o-Offshore
•-Inshore
'56 '57 '58 '59 '60
B. SEASONAL AND ANNUAL TRENDS IN FISHABLE BIOMASS - Offshore waters
'56 '57 '58 '59 '60
C. SEASONAL AND ANNUAL TRENDS IN FISHABLE BIOMASS - Inshore waters
-Closed season
'56 '57 '58 '59 '60
D. MODAL-SIZE DISTRIBUTION: Offshore Landings* (Dominant mode-□)
WHITE SHRIMP STATIST
LOUISIANA COAST
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1956 1957 1958 1959 1960 1961

FIGURE 4. White shrimp catch and population statistics — Louisiana co (statistical subareas 13-17), 1956-1960.
*Numbers of whole shrimp per pound

might consider evaluating the degree of relationship between the time-ser of a species commercial biomass and the time-series of tidal heights, fres water influx, etc. in inshore or estuarine waters where the common spec pass through critical stages in their early development. The time lag, course, would be roughly the average amount of time lapsing between t mid-point in each age class's estuarine phase and the point in time when attains maximum biomass in transition or offshore waters. In this instan the obvious hypothesis is that the survival of each season's reproduction most closely associated with the quality of environmental conditions duri estuarine phases. Analyses of this sort have not yet been attempted mai because of the relative shortness of biomass time-series.

A comparison of the time-series in Figures 4B and 4C reveals some similar and thereby corroborates the expected relationship between the two. Ma seasonal peaks occurred at about the same time, there being some indicati that those on the inshore biomass curve slightly preceded those on the offsh curve. The mean amplitude of oscillations on the inshore curve appreciat exceeded that of oscillations on the other, this reflecting expected mortal during migration from inshore to offshore waters. Secondary peaks appear on the offshore curve in the first half of each calendar year suggest for wh

shrimp a reproductive pattern involving semiannual periods of heightened spawning activity. Also of special interest is the fact that the sharp drop in 1957's yield was not paralleled by a correspondingly abrupt drop in biomass, at least in the offshore population phase.

Age Structure - Fished Population

All commercial shrimp are sold and bought on the basis of their relative size with the largest specimens bringing the highest price. When landings are broken down according to the sizes of shrimp comprising them, the resulting distribution affords some insight into the age structure of the population being fished — provided that the landings are reasonably representative of the population's defined biomass. Any effects of differential bias due to (1) fisherman or gear selectivity; (2) non-uniform distribution of fishing effort with respect to stratification by age within the fished population; (3) minimum-size restrictions; and (4) varying size-grading practices must be assumed negligible, or at least constant in time.

Totals for the seven or eight size categories into which commercial shrimp landings are separated give weight frequency curves whose modes, it is believed, roughly delineate the age classes or "broods" making up the exploited biomass. Monthly weight frequency distributions for each coastal section are obtained by summing, within each size category, the landings from each subarea and depth zone. Plotted serially and fitted with smooth curves, the size-distribution modes trace the progress, from recruitment to disappearance from the fishery, of age classes arising in successive periods of heightened spawning activity. The curve for each class is the typical sigmoid curve describing population growth in terms of weight. For purposes of the following discussion, its disposition with respect to the ordinate is irrelevant, the mid-points of size classes being arranged arbitrarily thereon.

Good representation of vulnerable sizes in landings from offshore waters in the Louisiana Coast area provides a synoptic picture of age structure in what is considered the nucleus of northern Gulf of Mexico white shrimp stocks (Figure 4D). Heightened spawning in November-December and in June-July may be inferred, respectively, from offshore recruitment surges in May-June (light arrows) and again in November-December (dark arrows). Evidence for semiannual peaks of spawning activity can hardly be refuted since this phenomenon has now been shown to recur over a reasonably long period of time. A similar pattern has also been noted for white shrimp stocks elsewhere in the northern Gulf. Plots of modal-sizes from weight frequencies of inshore landings yield essentially the same picture except that dominant modes usually represent smaller shrimp.

Year-to-year variation in the magnitude of peak spawning activity as well as in the chronology of recruitment is obvious from the picture presented in Figure 4D. When reproductive patterns for white shrimp stocks in northeastern and northwestern Gulf areas are compared, it is seen that members of early-season broods (dark arrows) dominate fisheries in both areas but that they attain particular significance in the northwestern Gulf. Secondary yield and biomass modes occurring in May or June (*cf* Figures 4A, 4B, and 4C) are attributed to late-season broods supplementing portions of both the preceding early-season brood and the late-season brood produced 1 year earlier. Spawning populations giving rise to early- and late-season broods are believed to be predominated by survivors of the previous year's corresponding

broods. The degree of predominance appears to vary widely, however, bei largely dependent upon the relative initial strength and subsequent surviv of each half-year class making up a spawning population.

The Greatly Diminished Fishery of 1957

Information such as that depicted in Figure 4D together with, in this cas tentative knowledge of the time lapse and spatial distribution of development stages between hatching and recruitment to the offshore fishery, provides biological framework within which the cause(s) of fluctuations in shrim yields can be theorized. Of particular interest is the observation that shrim forthcoming during periods of heightened spawning in November-Decemb and in June-July may be expected to occupy the inshore nursery groun during, respectively, February-April and August-October. Though there some question as to the extent to which representatives of the late-seas spawning mode utilize inshore areas during the winter months immediate following, it is well known that such areas harbor in great quantity repr sentatives of the early-season spawning peak during late summer and fa Based on the over-all percentage size composition figures given earlier, insho landings accumulating over the last 5 months of each calendar year are cor posed largely of fast-growing members of the same year's early-season broo On the other hand, offshore landings consist mainly of members of the pr vious year's early-season brood plus any residuals of earlier broods, includi those of the previous year's late-season brood. Some overlap obviously occu since many individuals attaining fishable size in inshore waters are simu taneously in the process of migrating to offshore waters.

Coinciding with periods of peak inshore and nearshore concentrations (1) migrating juvenile white shrimp representing 1956's late-season broo and (2) late postlarvae and juveniles representing 1957's early-season broo was the occurrence of intensive tropical storms. Thought to have wrought t most damage to inshore and nearshore biota was Hurricane "Audrey" whi hit the Gulf coast just east of the Texas-Louisiana border (statistical areas and 17) on June 27, 1957. Storm surges brought tides of almost 14 feet abo m.s.l. in the Cameron, Louisiana, area; 4 feet above m.s.l. in Garden Isla Bay, 250 miles to the east; and 3 feet above m.s.l. at Port Aransas, 220 mil to the west. Low-lying areas in Louisiana were inundated up to 25 miles inla (Moore et al., 1957). Tropical storm "Bertha," not quite attaining hurrica intensity, shortly followed "Audrey," striking the coast in the same gene area on August 9. The highest accompanying tide, 4.7 feet above m.s.l., w recorded in Vermilion Bay. Although the mechanics involved are obscure, is conceivable that factors such as: extended periods of high salinity, destru tion of cover and food supplies, and excessive turbulence, all induced extraordinarily high tides, acted corporately to disperse and otherwise exe greater-than-normal mortality in white shrimp populations during vulnerab inshore phases.

Excessive fishing on spawning populations giving rise to early- and la season broods in 1956 and early-season broods in 1957, is discounted as contributing factor. Comparatively speaking, indices of mean biomass f offshore and inshore population phases suggested that white shrimp spawni potential in 1956 and early 1957 was more than adequate (*cf* Figures 4A a 4B). A low inshore biomass in late 1957 did suggest, however, the low su vival of that year's early-season brood during pre-juvenile stages.

Although effort expenditure fell off during the latter half of 1957, the drop was not sufficient to account for the disproportionate drop in landings. Effort expended on inshore and offshore grounds in the Louisiana Coast area during July-December, 1957, was 72 and 51 per cent, respectively, of that expended during the same period in 1956. Corresponding landings, on the other hand, were only 25 and 36 per cent of those recorded in 1956. In Texas, about the same amount of effort expended in offshore waters during the latter half of 1956 was recorded for 1957, but the corresponding white shrimp catch declined 43 per cent. By way of contrast, the Texas inshore fishery doubled its production over the same period with only a 55-per cent increase in effort expenditure. Most of this, however, came from bays along the southern half of the Texas coast, well outside the main area of storm damage.

Record low white shrimp landings from Louisiana waters in 1957 must therefore be ascribed more to a real (though momentary) decline in population strength than to relaxed exploitation during a period when the white shrimp normally attains peak density and avialability. The import of factors contributing to this decline is also manifested in the magnitude of the following year's landings. Thus, notwithstanding an immediate return of effort expenditure to its 1956 level (Figure 3), restoration of landings to their former (1956) level has lagged for 3 years.

The Fishery's Recovery

The effectiveness of newly enacted closed-season laws (inshore waters: Louisiana, 1958) in bringing about the fishery's recovery would appear debatable. Most noteworthy, perhaps is the fact that these closures generally coincide with or occur shortly after seasonal ebbs in the white shrimp's nursery ground phases. Records show that in years prior to this more rigidly enforced closed-season law (1956-1958), white shrimp landings (inshore) over the period December-April averaged but 6 per cent of each year's total. The closed season, mid-December through April, in effect, protects (1) residuals of early-season broods, most of whose representatives will have already passed to offshore waters by the time the fishing season closes, and (2) late-season broods, the postlarvae of which begin to move into inshore areas at about the same time. Most members of the less important late-season broods will have attained commercial size when the fishing season reopens in May. Though now protected in inshore areas, these broods have never contributed as significantly to inshore or offshore fisheries as have their early-season counterparts.

Conversely, early-season broods which are fished heavily in inshore waters during late August through November are the same broods dominating (for the most part in the following year) the offshore fishery which reaches peak production almost simultaneously. For all practical purposes, they support the white shrimp fishery but are not now afforded anywhere near the extensive protection given late-season broods.[4] Nor is additional protection called for unless a significant relationship between fishing rate and brood size (or recruitment) manifests itself.

Available statistics do not permit establishing whether or not such a relationship prevailed. But despite improved yields, the white shrimp stock in the

[4]The closed season, early July to mid-August, offers early-season white shrimp broods protection from excessive fishing on pre-commercial sizes. Inshore production of small brown shrimp has not been affected by either closure.

northwestern Gulf has shown little sign of recuperating from the reduc
level of 1957. This could be due to too heavy fishing pressure having be
exerted too soon after an extreme population setback. If each year's do
nant early-season broods are roughly separated by analyzing only those statist
for the months July-December, plots of mean annual biomass against c
responding fishing intensity mildly suggest such a possibility (Figure 5).
Louisiana's offshore waters, quadrupled fishing intensity in 1957 had
apparent effect of delaying initiation of a recovery trend until the follow
year. Unfortunately for the white shrimp, 1958 was a year in which rec
high shrimp prices induced extra-heavy fishing pressure. Most of this w
directed at the brown shrimp with the low-level white shrimp populati
suffering coincidentally. Effects of exploitation inshore are also well illustra

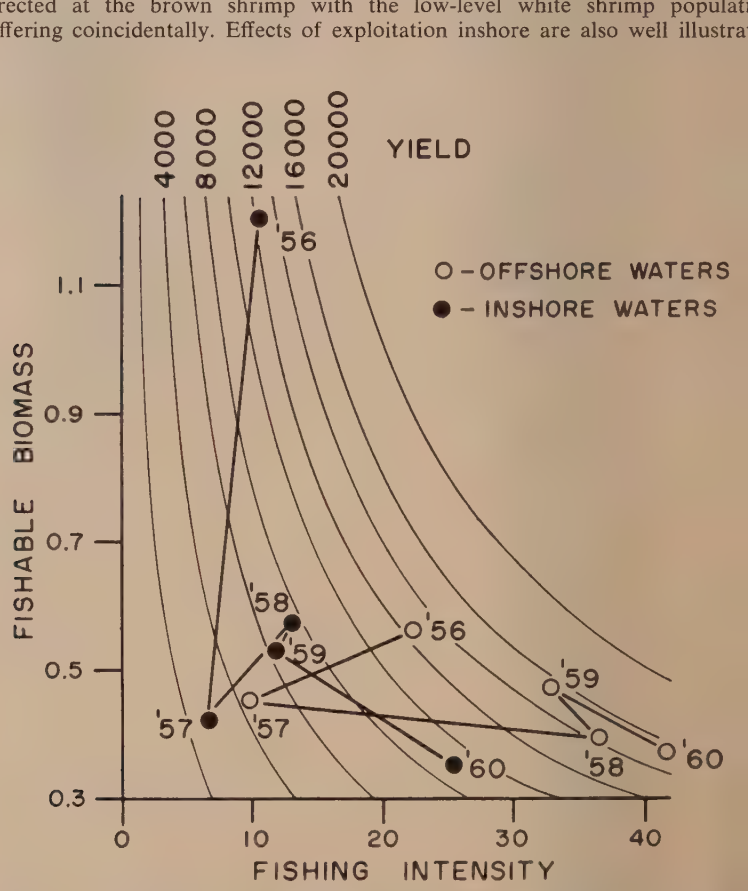

FIGURE 5. Relationship between exploitable biomass and degree of fishi
intensity. [Data refer to dominant half-year classes (successive early-seas
broods) of white shrimp in the Louisiana Coast area (1956-1960) as isolat
through analysis of commercial fishery statistics combined over the mon
July-December only.]

and, in fact, may have controlled the pattern which developed. A doubling of inshore fishing intensity in 1958 seemingly contributed to the decline in the offshore population phase the same year, and in itself may have stifled an earlier upsurge in the over-all population. Relaxation of fishing pressure on the inshore phase in 1959 resulted in concomitant recovery in offshore (spawning) population phases. A more comprehensive analysis would have to incorporate precise knowledge of what proportion of each year's (last semester) offshore biomass consisted of (1) the same and (2) the previous year's reproduction.

Data for 1961 are incomplete but those for 1960 indicate a low inshore biomass as well as a reduced offshore biomass late that year. The former condition forewarned a reduced offshore (commercial) biomass while the latter intimated a reduced spawning population and hence a small early-season brood the following year. Both conditions portended a generally diminished production in late 1961. Probable adverse effects of the high fishing intensity in offshore waters in 1960 will likely not be noticed until late 1962. Meanwhile, it is believed that the high exploitation of 1960's early-season brood will be largely responsible for a marked drop in 1961's offshore production.

In summary, the question is not so much one of whether, following periods of high natural mortality, fishing intensity should be regulated at all, but one of deciding at what season such regulation would be most effective. Little benefit can be expected from suspending fishing in inshore waters when population phases there are at minimal density. On the other hand, closed seasons or regulated fishing in offshore waters supporting multi-species fisheries are, practically speaking, out of the question altogether.

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those changes which are seasonal in nature and those which may be due to annual or longer periodic cycles, and (2) to interpret changes in the biota resulting from man's activities. Studies are being made of physical change due to dredge-and-fill operations and of chemical change due to domestic, agricultural and industrial wastes. The effects of these wastes are being identified (1) by establishing toxity levels and (2) by measuring changes in plankton productivity and storage of radionuclides in invertebrate fauna.

Biological features being studied and methods used to estimate their parameters are primary productivity (plankton volumes and plankton pigments) setting rates of sedentary organisms (fouling plates), distribution and population densities of benthic animals (dredging), distribution and population densities of pelagic animals (trawling), and distribution of benthic animals rarely found in ordinary field samples because of severe predation (protected habitat boxes). Hydrographic features being studied are salinity, water temperature, pH, and visibility index (Secchi disk).

RESEARCH AT THE GALVESTON BIOLOGICAL LABORATORY

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INTRODUCTION

The Bureau of Commercial Fisheries Biological Laboratory at Galveston, Texas, is currently engaged in a broad program of marine research directed at appraising commercial, shallow-water fish and shellfish populations. The determination of governing factors and the manner in which they interact to shape these populations constitutes the program's central theme. Inshore waters from the Florida Keys to the Rio Grande and, in general, shelf waters throughout the Gulf of Mexico, comprise the Laboratory's geographical area of responsibility. Most interest centers upon the valuable penaeid shrimps and, collectively, a wide variety of demersal and and pelagic "industrial" fishes. All research is conducted and the results disseminated to aid responsible agencies in regulating the exploitation of these and other fishery resources.

FACILITIES

A professional staff of 32 scientists is housed at or operates from the Galveston laboratory and three field stations located at Pascagoula, Mississippi, and St. Petersburg Beach and Miami, Florida. Major facilities now include a 68,000-gallon-capacity recirculating sea-water system, a well equipped chemistry laboratory, and a fairly large library. A substantial circulating sea-water laboratory is in the final stages of construction at Galveston's East Beach Lagoon; several controllable-temperature rooms are in the preconstruction stage at the Galveston laboratory; and a 90-foot steel-hulled research vessel is undergoing preliminary design. Vessels currently employed to gather biological, physical, and chemical data in the open Gulf are chartered for 6-month or shorter periods from private individuals or concerns, or from the Bureau's exploratory fishing activity based at Pascagoula, Mississippi. Two diesel-powered launches and several smaller outboard craft are used for sampling inshore waters in the Galveston, Tampa, and Key West areas.

Subdivided into five sections referred to as "programs" (previously "investigations"), the over-all research schedule of the Galveston Biological Laboratory stresses the quantitative approach to problems concerning utilization of the Gulf's commercial fishery resources. In one way or another, each program complements the others.

SHRIMP FISHERY PROGRAM

The largest of these programs, and at the moment the most important, is the Shrimp Fishery Program which has been in existence about three years. Its activities may best be described in terms of the four projects now comprising it. These have been organized in relation to four distinct phases in shrimp population development, each of which commands special attention. One project deals with the evaluation as to size, reproductive potential, and distribution of spawning populations, as well as the extent and chronology of spawning activity itself. Each of the three major shrimp species along with several minor species are being studied from these standpoints in the western Gulf of Mexico. Systematic sampling with standard gear and histological analysis of shrimp reproductive organs are included among the tools facilitating this important inventory.

Measurements permitting estimation of parameters which may characterize the environment of each species spawning populations are being taken simultaneously.

Closely related to the foregoing is a project concerned with measuring the initial abundance, distribution, and survival of the meroplanktonic shrimp larvae and postlarvae. Systematic sampling with standard (specially designed) gear is likewise one of its features. A major consideration here is the question of long standing among shrimp biologists: What are the mechanisms controlling movement of certain penaeid larvae from offshore spawning to inshore nursery grounds? To determine what role in the transport of larvae, if any, is played by current prevailing at or immediately following periods of heightened spawning activity, observation of direction and velocity of ocean currents constitutes an integral feature of regularly scheduled sampling cruises. The flow method of determining water-mass movement is currently used but will be periodically supplemented in the near future by path methods.

Tied in very closely with the above project is a sizable study (or subproject) concerned with the taxonomy of immature Penaeidae, most species until recently having been practically impossible to differentiate during larval and early postlarval stages. Greatest success here has resulted from rearing and describing larvae hatched from eggs spawned in laboratory aquaria by parents of known identity. Early larval stages of at least three species are now being documented.

The third project undertakes surveillance of inshore (or juvenile) population phases. Utilization of shallow estuarine waters appears, to a great extent, characteristic of the genus Penaeus, representatives of which sustain the Gulf's commercial shrimp fishery. Research on their dynamics is facilitated by the availability of production and effort statistics emanating from the rapidly expanding bait fisheries that these juvenile populations support. In cooperation with the Bureau's Branch of Statistics, such data are collected routinely in the Galveston and Tampa Bay areas.

Studies of the dynamics of "fishable" population segments, those consisting largely of adult, commercial size shrimp, are carried out by the fourth and final project. These studies could not be executed to the desired degree without the services of the Branch of Statistics which provides the necessary sampling data, namely, detailed commercial fishery

statistics. It should be pointed out, however, that the approach to parameter estimation employing fishery statistics is being increasingly supplemented by the experimental or mark-recapture approach in which dyes or tags are used as shrimp-marking agents. Objectives here include (1) establishment of the chronological relationship between population size and fishing intensity alone, and together with certain specified natural variables; (2) delineation of the relationship between natural mortality and population growth, i.e., determination of the expected point in spawning class development where both parameters balance each other, this signifying maximum attainable biomass; and, (3) contingent upon how well the above relationships are described, development of techniques for short-range prediction of the magnitude of available supply.

ESTUARINE PROGRAM

Consisting of three projects, this recently formulated program arose out of an apparent need to investigate and assess the effects on shallow-water fishery resources of man-induced modifications in the extensive Gulf coast marshes. Well established is the fact that most of the Gulf's commercially important crustaceans, molluscans, and fishes spend all or a large portion of their lives in these shallow estuarine areas. Although adverse effects directly attributable to man have not yet been specifically documented as such, it is easily conceivable that they will occur and be detected if these modifications continue at their present pace. The possibility that some changes in the estuarine environment will enhance rather than reduce the potential of certain resources is not being discounted.

To provide a basis for making future comparisons, one project in the Estuarine Program is wholly concerned with preparing a catalog or inventory of Gulf coast estuaries as they now exist. This involves searching out, organizing, and integrating all published data describing such areas. Features being considered range from an estuarine area's geology and climatology to its ecology and relative worth in terms of the average yields of its biological populations. An atlas of Texas coastal marshes in nearing completion.

Another project deals with the ecology of coastal marshes as they provide habitat for the young of most and the adults of many commercial

fish and shellfish species. Study areas at present are the Galveston, and Tampa Bay complexes. Here again the over-all objectives are to assess, from long- and short-term standpoints, the effects that artificial and natural changes in the estuarine environment may have on the productivity of important fishery resources.

The remaining project serves to advise other government agencies of the probable manner, insofar as present knowledge of the tolerances of involved species permits, in which coastal engineering projects proposed by federal, state, and private organizations could affect the status of marine fishery resources. It further recommends, whenever feasible, modifications in proposed projects which would tend to mitigate expected damage. In so doing, close liaison is maintained between the U.S. Army Corps of Engineers, Bureau of Sport Fisheries and Wildlife, Gulf States Marine Fisheries Commission, state conservation agencies, and various commissions for the development of water resources.

INDUSTRIAL FISHERY PROGRAM

This three year old program, the smallest of those active, engages in research on shallow-water fishes collectively supporting "industrial" offshore fisheries in the north-central Gulf area. Personnel are located at Pascagoula, Mississippi, and Galveston, Texas. Areas and species having commercial fishery potential are being considered along with those now sustaining established fisheries. Objectives of the research at both Pascagoula and Galveston are, generally, (1) to describe the life histories of species dominating existent and potential fisheries; (2) to ascertain their geographical and seasonal distribution; (3) to provide means for measuring and predicting their abundance; and (4) to define the mechanisms whereby artificial and natural factors govern their populations.

PHYSIOLOGY AND BEHAVIOR PROGRAM

Relegated to the confines of the laboratory, this program has the important function of evaluating the effects of and hence determining the relative tolerances of important commercial species to varying levels in

each of a variety of simulated environmental factors. Growth, survival, metabolic rate, and general performance are the experimental criteria employed. Factors being tested include temperature, salinity, diet, dissolved gases, and current speed. Facilitating experimentation with young shrimp and various fishes will be the temperature control rooms and circulating sea-water laboratory. Results of this research will be of great value in predicting the general effects of proposed engineering projects.

RED TIDE PROGRAM

Field investigation of the cause-effect relationships in Florida red-tide (Gymnodinium breve) outbreaks continues on a reduced scale in the Tampa Bay area. This activity is closely associated with laboratory studies on the biology of the causative agent conducted at the Galveston laboratory.

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Predation of the Dolly Varden, *Salvelinus malma*, on Young Salmons, *Oncorhynchus* spp., in an Estuary of Southeastern Alaska

KARL F. LAGLER AND ASA T. WRIGHT

Predation of the Dolly Varden, *Sa velinus malma*, on Young Salmon *Oncorhynchus* spp., in an Estua of Southeastern Alaska[1]

INTRODUCTION

Predation is a source of mortality to you salmon upon their first entry into salt wat Among the predators in Alaska is a char, t Dolly Varden, *Salvelinus malma*, which habits many of the same waters as you salmon (Clemens and Wilby, 1949). The p pose of this study was to examine the food the Dolly Varden when it was associated w young pink (*Oncorhynchus gorbuscha*), chu (*O. keta*), and coho (*O. kisutch*) salm Field work centered in the estuary which ceives Sashin Creek at Little Port Walter n the southeastern extremity of Baranof Isla southeastern Alaska (56° 23′N, 134° 38– W). It was conducted from June 2 throu August 11, 1958.

AVAILABILITY OF YOUNG SALMONS TO DOLLY VARDEN

Young of the pink, chum, and coho sal ons move into the Little Port Walter estua during the spring and summer months, large part from Sashin Creek, its sole tri tary. Variations in time of entry and in nu bers and sizes of individuals depend, amo other things, on the species. In the estua the young encounter a new environment which they must adjust. Current, tempe ture, water chemistry, food, shelter, and va ety (and number) of predators are differe than in the stream. As they leave the stre mouth, the young concentrate in the upp least saline layers of water. Schools devel often mixed among the three species, and a most evident along the shores. Movem apparently may swing alternately toward a

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[1] Contribution from the U. S. Bureau of C mercial Fisheries and from the Department of F eries, The University of Michigan. Published w permission of the Director, U. S. Bureau of C mercial Fisheries.

away from the creek mouth. Perhaps this movement is a response to tides and their effects on the layering and currents of the fresh-water inflow.

From spring to summer, young salmon leave the original nursery estuary and spread along its adjacent coasts. They are abundant in the shelter of kelp beds and in protected coves. By midsummer the spread includes open water offshore, at least to distances as great as a half-dozen miles to the middle of Chatham Strait, into which the estuary at Little Port Walter opens. Here they are found (in sizes from about 4 to 9 inches) to approximately 10 fathoms (lampara catch). While growing to adulthood, young from Sashin Creek travel at least 120 linear miles into Chatham Strait (Elling and Macy, 1955) with the probability that greater distances are traversed (Pritchard, 1939).

Young of the three species of salmon were available to the Dolly Varden in the Little Port Walter estuary throughout the period of this study, June 1 through August 11, 1958. During this interval young of the pink, chum, and coho salmons were repeatedly observed and frequently collected by beach seine, scale-model salmon trap, tow net, and lampara in this water area. A reasonable assumption is that most of these salmon young entered the estuary from Sashin Creek, its only permanently flowing tributary. The lower 1,800 feet of this stream is accessible to ocean-run salmonids for spawning after they pass through the near-tide-level Sashin Creek weir seasonally maintained by the U. S. Bureau of Commercial Fisheries. Peak periods of entry of young-of-the-year salmons into the estuary in 1958[2] were: for the pink, April 8 to 29; for the chum, April 22 to May 6; and for the coho, May 4 to 13. Young pink salmon remained in the estuary at least until mid-July; young chum, at least until the end of July; and young coho, through August 11.[3]

While in the estuary young salmon appeared to grow rapidly. Apparently, however, they did not attain lengths during the summer months that would render them invulnerable to predation by the Dolly Varden. Upon being passed downstream through the weir into the estuary from March 9 through May 15, the average fork lengths (in millimeters) with little range of variation were: pink fry, 31; coho fry, 32, and fingerlings, 100; and chum fry, 35 (based on measurements by Jerrold M. Olsen). By June 10, young pinks in the estuary were ranging from 38 to 85 millimeters; coho, from 67 to 68; and chum, from 50 to 72. At the end of June, young pink salmon were 38 to 114 millimeters (fork length), coho fry and fingerlings combined 38 to 137 millimeters, and chum, 52 to 115 millimeters. No young of the pink salmon were collected in the estuary after July 1. Young chums were collected as late as July 23 at 131 millimeters fork length maximum and young coho as late as July 31 with a maximum fork length of 143 millimeters. These lengths are mostly within the range which the Dolly Varden can eat, as shown at the lower limit by the sizes of herring fry ingested (Table 1, average total length 34 millimeters, ranging from 18 to 62 millimeters for 322 specimens) and, at the upper limit, by the Pacific sand lance (139 millimeters total length of largest specimen eaten). However, the largest sand lance was eaten by a Dolly Varden only 386 millimeters in total length, whereas the largest Dolly that we collected was 476 millimeters in total length (1,152 grams), and the species attains at least 914 millimeters (36 inches, 20 pounds; Carl and Clemens, 1948) in more southerly waters. There are no Alaskan records of this size.

TABLE 1.—*Mean calculated total lengths of the Dolly Varden from Little Port Walter estuary, Alaska, summer, 1958*[1]

Age in years	Calculated length at annuli (millimeters)				
	I	II	III	IV	V
1	85	–	–	–	–
2	91	151	–	–	–
3	95	153	215	–	–
4	88	162	233	304	–
5	96	167	243	318	388
Mean	94	157	230	310	388
Standard deviation of mean	10	15	24	21	17

[1] Based on 20 specimens of each age selected from among the individuals examined for food. The body–scale regression was $y = 9.998 + 0.1449\,x$. From Wright, Asa T., 1960. Age and growth of the Dolly Varden char (*Salvelinus malma* Walbaum) in southeastern Alaska. 18 pp. M.S. Thesis. University of Michigan Libraries. Unpublished.

FOOD OF DOLLY VARDEN

Food habits of 183 adult and subadult individuals of the Dolly Varden collected with other fishes by the authors in the Little Port Walter estuary in 1958 were examined. The

[2] Weir counts by Jerrold M. Olsen.

[3] Lagler, Karl F. (1959) Field report on 1958 studies of early saltwater life of the pink salmon, Port Walter region, Baranof Island, Alaska. Juneau, U. S. Bur. Comm. Fish., 33 pp. (offset).

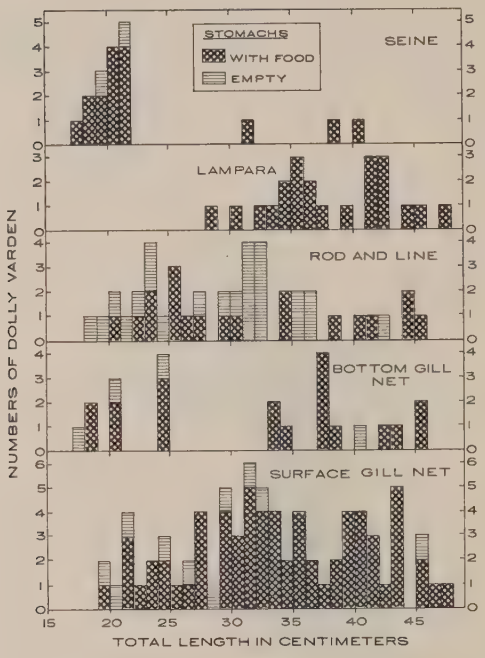

FIGURE 1.—Relationships among method of collection, size of the Dolly Varden captured, and presence or absence of food in stomachs.

char were captured by various methods (Figure 1): 54 percent by gill net; 10 percent by beach seine; 12 percent by lampara net; and 24 percent by rod and line. In June, 51 percent of the total were taken, and in July 45 percent. The remainder was caught during the first 9 days of August.

Of the 183 stomachs of the Dolly Varden examined, 40 were empty (Figure 1). The 143 individuals with food ranged in size (respectively, fork length and total length in millimeters and fresh total weight in grams) as follows: smallest 148, 168, 45; mean, 309, 329, 430; largest, 452, 476, 1,152. Age groups represented were yearling through 5-year-old (Table 1).

The principal foods by volume were capelin (78.8 percent), Pacific sand lance (7.1 percent), polychaete worms (4.7 percent), and Pacific herring (4.0 percent) (Table 2).[4] The frequency of occurrence of the various items was: capelin (49.7 percent); sand lance (18.9 percent); herring (16.1 percent) (Table 2). Crustaceans occurred in 11.8 a polychaetes in 5.6 percent of the stomachs.

[4] Identifications were based primarily on Wilimovsky (1958), Provisional keys to the fishes of Alaska. Juneau, U. S. Fish and Wildlife Service Fishery Research Laboratory, 113 pp. (offset).

TABLE 2.—*Stomach contents (1,386.3 milliliters) 143 Dolly Varden char, from Little Port Wal estuary, Alaska, summer, 1958*

Food item	Approximate number of individuals of food item	Percentage of total volume of food	Percentage frequency o occurrence
Capelin	275	78.8	49.7
Sand lance	111	7.1	18.9
Herring	328	4.0	16.1
Salmon young	5	1.0	2.8
Fish remains	47[1]	2.3	25.9[1]
Crustaceans	1,183	2.0	11.8
Polychaete worms	32	4.7	5.6

[1] Includes a trace (less than 0.1 milliliter) of a lipa in one stomach.

The capelin (*Mallotus villosus*) compos more than three-fourths of the volume stomach contents of the Dolly Varden in t estuary and was found in nearly one of eve two specimens studied. Total lengths of t capelin when alive could be measured or stored by estimation for 239 of the specime in the stomachs of the predator; for these t mean was 97.2 millimeters, and the range to 116 millimeters. This size range practica coincides with that of most of the adults the species taken from the same estuary seine and gill net (67 to 116 millimeters to length). The mean total length of the in viduals of the char that had eaten the capel was 381 millimeters, and the range, 261 476 millimeters.

The mean total length of the prey spe mens of the Pacific sand lance (*Ammodyt hexapterus*) was 70.5 millimeters, and th range, 34 to 139 millimeters. Dolly Vard in which they were taken averaged 291 mil meters and ranged from 182 to 462 millim ters, total length. Specimens of the sand lan that we collected by seine and gill net duri the same interval ranged from 48 to 159 m limeters, total length.

Since the Pacific herring (*Clupea hareng pallasi*) was eaten as larvae, it represent only a small part of the food but was pres in about one of every six char. The avera was about 14 larvae in each of their 23 pr ators (range, 1 to 51). As might be expecte the specimens of Dolly Varden that contain these small herring tended to be smaller th those feeding on the capelin or sand lan their average total length was 248.2 millim ters; range, 186 to 420 millimeters.

Various small crustaceans, mostly shrim were eaten in small quantity (2.0 percent

total food volume) with about the same frequency (16.1 percent) as larvae of the herring. Included were Mysidae and Euphausiidae (382 individuals, Eumalacostraca), Gammaridae (21, Amphipoda), and crab larvae (780, Brachyura; Decapoda). As for the small herring, a very few (6) of the predators accounted for most of the numbers consumed. The average total length of the 19 specimens of the Dolly Varden that had preyed on crustaceans was 249.1 millimeters, and the range, 187 to 450 millimeters.

Polychaete worms composed 4.7 percent of the total volume of food. They occurred in only 8 char. One char (434 millimeters, total length) contained most of the bulk as well as the specimens of the worms (25 worms, 45.6 milliliters in volume), in addition to one sand lance (3.0 milliliters).

Young salmon were available to the Dolly Varden in the estuary throughout the study period, although sampling of the char was after the seasonal peak of downstream migration of the young salmon and doubtless after some estuarine out-migration had occurred. Their remains were identified in only four (2.8 percent) char. This evidence does not, however, remove the Dolly Varden from concern as a significant predator of young salmons (Rounsefell, 1958). The Dolly, generally in smaller sizes than we sampled in the estuary, along with other known fry predators (Pritchard, 1936), including coho fingerlings, the introduced rainbow trout (*Salmo gairdneri*), and sculpins (*Cottus* sp.), inhabits Sashin Creek and doubtless preys upon the young as they emerge from the gravel and work their way downstream (as shown elsewhere by Pritchard, 1936). Furthermore, our sampling did not include the numerically changing aggregation of the char at the outfall of Sashin Creek into the estuary. This aggregation seemed to be well located for taking young salmon at the tidally variable point of their first contact with salt water. Here the concentration of both prospective predator and prey occasionally was relatively high. Unpublished field observations by Remo Riciputi at this site in 1959 showed a small school of about nine adults of the rainbow trout to be present at the Sashin Creek outfall, but no Dolly Varden. From April 10 to May 29, 1959, 232 adults of the Pacific herring were taken about the stream mouth. Whether or not they were predaceous on the young salmon was not determined.

FOOD OF ASSOCIATED FISHES

Late spring and early summer fish inhabitants of the Little Port Walter estuary and adjoining waters include numerous species sufficiently large and carnivorous to be potential predators of young salmon. Examinations of stomach contents of a few adults of each of the following fishes proved to be negative for salmon: Pacific cod (*Gadus macrocephalus*); walleye pollock (*Theragra chalcogrammus*); Pacific halibut (*Hippoglossus stenolepis*); kelp greenling (*Hexagrammos decagrammus*); rock greenling (*Hexagrammos superciliosus*); and black rockfish (*Sebastodes melanops*).

The hair seal (*Phoca r. richardii*) also occurs in the Little Port Walter estuary and adjacent bays. The numbers to be seen were never large in 1958, approximating about two per hour by an observer afloat along shore in a small outboard motorboat. The contents of the stomachs of three specimens examined were made up of remains of the Pacific herring.

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A Method of Estimating Mortality Rates from Change in Composition[1]

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ABSTRACT

This paper examines the problem of estimating mortality rates from knowledge of catch and of the change in composition caused by selective fishing on one of two classes of a closed population.

Estimators of fishing mortality in the presence and in the absence of natural mortality are given. An estimator of natural mortality is shown for the special case where final population size is known.

A numerical example illustrates the method. Certain problems are discussed and two types of application are suggested.

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INTRODUCTION

Changes in the composition of a fish population may provide estimates of important parameters. For instance, Widrig and Taft (1957) used changes in calculated length-at-age to find the fraction of a sardine (*Sardinops caerulea*) population present in one area at time 2 that came from another area since time 1. Murphy (1952) used a similar principle to estimate survival of silver salmon (*Oncorhynchus kisutch*) from the Eel River, California, during their third (final) year of life at sea. Here, factors causing early maturity selectively "remove" the males at age 2 and hence change the age and sex composition of the brood; escapement counts by age and sex provide the estimate.

Chapman (1955) derived the maximum likelihood estimators of initial population size when a harvest is selective for one class of a closed population which suffers no natural mortality during the catch interval. Classification can be for any observable character; examples are size, age, sex and color. Ricker (1958) describes the work of Chapman (1955) and Murphy (1952).

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The present paper examines the problem of estimating mortality rates from knowledge of catch and of the change in composition caused by selective removal of one class during the catch interval. From a mathematical viewpoint it simply shows how Chapman's (1955) fundamental work relates to the theory of fishing as developed by authors like Ricker (1958) and Beverton and Holt (1957).

The parallel to the theory of fishing was discovered incidentally in a search for ways to estimate mortality in a population of Pacific salmon (*Oncorhynchus*) exploited both by an offshore and inshore fishery. It soon was apparent that inexact knowledge of availability to offshore fishing rendered the method inappropriate for that problem. Nevertheless, the method itself is of interest for two reasons. First, catch is the one item of information accessible to relatively complete study. Second, Chapman (1955) indicated that extension of his basic theory to include open populations and natural mortality may not be too difficult.

Our objective is therefore to stimulate wider interest in the theory and practice of change-in-composition methods, with particular reference to estimation of mortality rates. First, we give a way to estimate fishing mortality when natural mortality is absent during the catch interval. Next, natural mortality is allowed and its effect on estimation of fishing rates examined. An estimator of natural mortality is then given for the special case of a known final population and of equal natural mortality rates on each of the two classes into which total population is divided. Finally, we discuss certain implications of the method and suggest possible applications.

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ESTIMATION OF FISHING MORTALITY WITH NATURAL MORTALITY ABSENT

Let a population be divided into two classes — such as small and large, or male and female — and designate these classes by X and Y. If classification is by length, for instance, gill nets of a particular mesh size will remove a higher fraction of those initially present in the X class (say) than in the Y class. Or anglers may take more sport fish from the X class because of a size limit. Now let:

N_{ij} = population present at time i in class j

1, 2 = subscripts designating start and end of the catch interval ($i=1, 2$)

x,y,z = subscripts respectively designating the X class, the Y class and the total population ($j=x,y,z$)

p_i = true fraction of total population in the X class at time i ($p_i = N_{ix}/N_{iz}$)

C_j = catch from class j in the catch interval ($i=1$ to $i=2$)

Assume that: (1) the p_i can be estimated from representative samples taken just before the start and just after the end of fishing, (2) fishing is selective for the X class, (3) the catches by class, C_j, are known, and (4) the population is closed.

Chapman (1955) shows that the change in p_i caused by selective removal leads to the following maximum likelihood estimators of initial population (at $i=1$, the start of fishing):

$$\hat{N}_{1x} = \frac{C_x - p_2 C_z}{p_1 - p_2} \quad \ldots (1)$$

$$\hat{N}_{1x} = \frac{p_1(C_x - p_2 C_z)}{p_1 - p_2} \quad \ldots (2)$$

Of course, the initial Y population is then found by difference.

From the standard equations of fishing theory as given in Beverton and Holt's (1957) notation, the average size of the X population in the absence of natural mortality is:

$$\overline{N}_x = \frac{N_{1x}(1 - e^{-F_x})}{F_x} \quad \ldots (3)$$

From Equation 3 (and recalling that catch is the product of fishing rate and average population, i.e., $C_x = F_x \overline{N}_x$):

$$N_{1x} = \frac{C_x}{(1 - e^{-F_x})} \quad \ldots (4)$$

Equating N_{1x} in Equation 4 with its estimate in Equation 2:

$$1 - e^{-\hat{F}_x} = \frac{C_x(p_1 - p_2)}{p_1(C_x - p_2 C_z)} \quad \ldots (5)$$

The complement of the left-hand side of Equation 5 can be found in any table of the descending exponential to give the estimated fishing rate, $\hat{F}_x$.

Estimation follows readily for F_y and F_z. Note that:

$$p_2 = \frac{N_{2x}}{\overline{N}_{2x}} = \frac{N_{1z}\, e^{-F_x}}{N_{1z}\, e^{-F_z}} = p_1 \left(\frac{e^{F_z}}{e^{F_x}} \right) \quad \ldots (6)$$

From Equation 6 an estimate of F_z is given by:

$$\hat{F}_z = F_x + \ln \left(\frac{p_2}{p_1} \right) \quad \ldots (7)$$

Also, parallel to Equation 6:

$$(1 - p_2) = \frac{N_{2y}}{N_{2z}} = \frac{N_{1y}\, e^{-F_y}}{N_{1z}\, e^{-F_z}} = (1 - p_1) \left(\frac{e^{F_z}}{e^{F_y}} \right) \quad \ldots (8)$$

Proceeding as for $\hat{F}_z$ as in Equation 7, then, Equation 8 becomes:

$$\hat{F}_y = F_z + \ln \left(\frac{1 - p_1}{1 - p_2} \right) \quad \ldots (9)$$

Equations 5, 7 and 9 can therefore be used to get fishing rates for the X, Y and total populations, respectively, from observed catch data and from the change in composition as measured by representative samples of the p_i when mortality is absent.

ESTIMATION OF FISHING MORTALITY WITH NATURAL MORTALITY PRESENT

For a given set of fishing rates and initial populations the catch will be lower, of course, when natural mortality is present. The change-in-composition method is based on catches which reflect the effects of any natural mortality; hence it is worthwhile to examine the effects of this mortality on the above estimates of fishing rates.

In the first case, suppose natural mortality to operate at the same rate, M on both the X and Y populations. Designating by the prime symbol (′) the final populations N'_{2z} and N'_{2x} which are now less than the final populations N_{2z} and N_{2x} that occurred when M was zero, note that:

$$p'_2 = \frac{N'_{2x}}{N'_{2z}} = \frac{N_{1x}\, e^{-(F_x+M)}}{N_{1z}\, e^{-(F_z+M)}} = p_1 \left(\frac{e^{F_z}}{e^{F_x}} \right) \qquad \ldots (10)$$

Equation 10 is identical to Equation 6; thus the final fraction of total population in the X class is independent of natural mortality, provided $M_x = M_y$. Recall also that p_1, measured before the start of fishing, cannot be affected by natural deaths in the following catch interval.

The question is how Equations 5, 7 and 9 are affected by non-zero natural mortality when $M_x = M_y$. If Equation 5, for instance, remains unbiased, one can write:

$$\frac{C_x(p_1 - p_2)}{p_1(C_x - p_2 C_z)} = \frac{C'_x(p_1 - p_2)}{p_1(C'_x - p_2 C'_z)},$$

where the primes designate the new catches made with natural mortality present. Recalling that the p_i are independent of natural mortality, the expression just above can be written for present purposes as a conditional identity by: (1) multiplying it by $p_1/(p_1 - p_2)$, (2) inverting and subtracting unity from both sides, (3) multiplying by −1 and cancelling p_2, and (4) inverting back again. This results in:

$$\frac{C_x}{C_z} \stackrel{?}{=} \frac{C'_x}{C'_z} \qquad \ldots (11)$$

We found that Equation 11 is not a general identity, but discovered by numerical models that these catch ratios are equal for practical purposes (to two-place accuracy). One such model is shown in Table I. The second column of Table I uses symbols given previously and includes certain definitions for readers unfamiliar with the theory of fishing.

A value of $p_i = 0.7$ was assigned to the initial total population of 10,000 fish to give initial numbers of 7000 and 3000 in the X and Y populations, respectively. To the latter were assigned fishing rates of $F_z = 0.6$ and $F_y = 0.2$ as M varied from 0 to 0.5. The value of $F_z = 0.46$ was found from Equation 7 after p_2 was computed, and checked by dividing the average total population by its catch. Otherwise, the calculations of Table I are self-explanatory.

The slight downward bias (−2 for total population, −1 for the X and Y populations) in initial population estimates made for $M = 0$ from Equations 1 and 2 is due only to rounding in the course of calculation. The feature of interest is that the estimates of fishing rates—the $\hat{F}_z$, $\hat{F}_x$ and $\hat{F}_y$—are independent of M and

equal to the true rates despite the increasing bias in initial population estimates as M approaches 0.5.

The next case occurs when natural mortality operates at different rates on the X and Y population ($M_x \neq M_y$). Here, it is intuitively reasonable to expect bias in using Equations 5, 7 and 9; we wish to get a notion of its magnitude.

Figure 1 shows the bias in using Equation 5 when M_x and M_y each vary in increments of 0.1 from 0 to 0.5. The calculations were carried out with the same N_{ij}, F_j and p_i as in Table I.

The bias shown in figure 1 is for practical purposes a linear function of the difference between fishing rates in the X and Y populations (rather than of their absolute magnitude). For a given difference this bias is lower when natural mortality in the dominant X population exceeds that in the smaller Y population.

ESTIMATION OF NATURAL MORTALITY WITH FINAL POPULATION KNOWN

In special circumstances, as in certain runs of anadromous species, the final population may be known. One can then estimate natural mortality in the first case above ($M_x = M_y$).

Once the fishing rates are estimated without bias, division of known catch by estimated fishing rate gives an unbiased estimate of average population:

$$\hat{\bar{N}}_j = \frac{C_j}{\hat{F}_j} \qquad \ldots (12)$$

The general expression for average size of the j^{th} population is:

$$\bar{N}_j = \frac{N_{1j}\left[1 - e^{-(F_j+M)}\right]}{F_j+M}$$

On solving for initial population, this becomes:

$$N_{1j} = \frac{C_j + M\bar{N}_j}{1 - e^{-(F_j+M)}} \qquad \ldots (13)$$

Initial population can also be put in terms of the known final population:

$$N_{2j} = N_{1j}\, e^{-(F_j+M)}$$

whence

$$N_{1j} = \frac{N_{2j}}{e^{-(F_j+M)}} \qquad \ldots (14)$$

The right-hand sides of Equations 13 and 14 can be equated; expanding and simplifying the resulting expression gives:

$$N_{2j}\, e^{M} - \bar{N}_j e^{-F_j M} = e^{-F_j}(C_j + N_{2j}) \qquad \ldots (15)$$

With N_{2j}, F_j and C_j known, trial values for M can be inserted in the left-hand side of Equation 15 until the known quantity on the right-hand side is closely approximated. Referring to Table 1, for instance, suppose that $N_{2z} = 4666$ were known and one wished to estimate M from Equation 15. Inserting numerical values from the sixth column of Table 1:

$$4666\, e^{M} - \bar{N}_z\, e^{-0.46} M = e^{-0.46}(3241 + 4666)$$

TABLE I. Numerical model to illustrate computation of fishing rates by the change-in-composition method described in the text.

Quantity	Symbol		Numerical values					
1. Initial total population	N_{1z}		10000	10000	10000	10000	10000	10000
2. Fraction of total population in X class	p_1		0.7	0.7	0.7	0.7	0.7	0.7
3. Initial X population	p_1N_{1z}		7000	7000	7000	7000	7000	7000
4. Initial Y population	$(1-p_1)N_{1z}$		3000	3000	3000	3000	7000	3000
5. Instantaneous rate of natural mortality	M		0	0.1	0.2	0.3	0.4	0.5
6. Instantaneous fishing rate on X population	F_x		0.6	0.6	0.6	0.6	0.6	0.6
7. Instantaneous fishing rate on Y population	F_y		0.2	0.2	0.2	0.2	0.2	0.2
8. Instantaneous fishing rate on total population	F_z		0.46[a]	0.46[a]	0.46[a]	0.46[a]	0.46[a]	0.46[a]
9. Catch of j-type fish $(j=x,y)$[b]	C_j	$(j=x)$ $(j=y)$	3158 544	3020 518	2891 495	2769 472	2655 451	2547 431
10. Total catch	C_x+C_y		3702	3538	3386	3241	3106	2978
11. Natural deaths of j-type fish[c]	D_j	$(j=x)$ $(j=y)$	0 0	503 259	964 495	1385 708	1770 902	2123 1079
12. Total natural deaths	D_x+D_y		0	762	1459	2093	2672	3202
13. Final X population	$N_{2x}=N_{1x}-C_x-D_x$		3842	3477	3145	2846	2575	2330
14. Final Y population	$N_{2y}=N_{1y}-C_y-D_y$		2456	2223	2010	1820	1647	1490
15. Final total population	$N_{2x}+N_{2y}$		6298	5710	5155	4666	4222	3820
16. Fraction of final total population in X class	$p_2=\frac{N_{2x}}{N_{2x}+N_{2y}}$		0.61	0.61	0.61	0.61	0.61	0.61

TABLE I. (continued)

Quantity	Symbol	Numerical values					
17. Estimate of initial total population	$(C_x - p_2C_2)/(p_1 - p_2)$	9998	9576	9173	8800	8448	8116
18. Estimate of initial X population	$p_1(C_x - p_2C_2)/(p_1 - p_2)$	6999	6703	6421	6160	5914	5681
19. Estimate of initial Y population	Item 17 minus item 18	2999	2873	2752	2640	2534	3435
20. Estimate of seasonal fishing mortality rate for X population	$(1 - e^{-\hat{F}_x}) = \frac{C_x(p_1 - p_2)}{p_1(C_x - p_2C_x)}$	0.45	0.45	0.45	0.45	0.45	0.45
21. Estimate of instantenous fishing rate for X population	$\hat{F}_x$	0.6	0.6	0.6	0.6	0.6	0.6
22. Estimate of instantaneous fishing rate for total population	$\hat{F}_s = \hat{F}_x + \ln\left(\frac{p_2}{p_1}\right)$	0.46	0.46	0.46	0.46	0.46	0.46
23. Estimate of instantaneous fishing rate for Y population	$\hat{F}_y = \hat{F}_s + \ln\left(\frac{1-p_1}{1-p_2}\right)$	0.2	0.2	0.2	0.2	0.2	0.2

[a] An average value for any one "experiment". F_x and F_y are fixed; yet F_s decreases from 0.480 at the start to 0.444 after the last removal (which reduces p_2 to 0.61), since the more vulnerable X population declines faster than the Y population.

[b] $C_j = \frac{F_j N_{1j}\left[1 - e^{-(F_j + M)}\right]}{F_j + M}$

[c] $D_j = \frac{M N_{1j}\left[1 - e^{-(F_j + M)}\right]}{F_j + M}$

Of course (recalling Equation 12):

$$\hat{N}_z = \hat{N}_x + \hat{N}_y = \frac{C_x}{\hat{F}_x} + \frac{C_y}{\hat{F}_y} = \frac{2769}{0.6} + \frac{472}{0.2} = 6975$$

On substitution of 6975 for $\hat{N}_z$:

$$4666\ e^M - (6975)\ (0.63)M = (7907)\ (0.63),$$

$$4666\ e^M - 4394M = 4981$$

A trial value of $M = 0.2$ leads to:

$$(4661)\ (1.22) - (4394)\ (0.2) = 4814$$

Since $4814 < 4981$, try a larger M (say $M = 0.3$). This gives:

$$(4666)\ (1.35) - (4394\ (0.3) = 4981$$

Thus $M = 0.3$ is the correct value, as verified from Table I.

DISCUSSION

Among the requirements for practical application of the method just described is that fishing be intensive and selective enough to make p_2 significantly less than p_1. Of course, when X and Y are *size* classes and individuals are actively growing in the catch interval, the effects of growth require evaluation. Also, one must face the problem of obtaining representative samples at times 1 and 2 to estimate the p_i. For gill net fisheries, at least, recent contributions by Holt (1957), Olson (1959) and McCombie and Fry (1960) to the theory of gill net selection strongly indicate that one can achieve truly representative sampling of the available population.

A more serious problem might occur when p_2 is observed to be significantly less than p_1 (hence indicating feasibility of the method), but where the $\hat{p}_i$ are not measured on the *same* total population, no matter how accurately they measure the p_i on the total populations available at time i. If size is the criterion, for instance, p_2 might be lower than p_1 both from selective fishing on the X population *and* from an influx of small or departure of large fish during the catch interval. In this case estimation of fishing rates by Equations 5, 7 and 9 is not valid. Were estimates of availability made — as from the methods of Widrig (1954) or Gulland (1955) — one perhaps could set up models of initial population size and availability (in combination with fishing rates estimated for full availability) that *could* give the observed change in p_i, then attempt iterative solutions for the whole system with whatever auxiliary information was at hand. However, these complications will in general require extension of the theory to open populations as implied by Chapman (1955).

Whether it will be reasonable to assume equal rates of natural mortality on the X and Y population depends on the nature of the classification made. Of course, X and Y can be whatever arbitrary classes render this assumption most reasonable. The problem of class differences in natural mortality may not be serious in practice. In the first place, natural mortality usually is low for a

single fishing season. Secondly, Fig. 1 shows the bias in $\hat{F}_x$ to be low (0.1) relative to the high (for a single fishing season) difference of 0.3 between M_x and M_y.

One obvious application might be to a closed population of tagged fish subsequently captured by a gear selective for size or some other character. In this case, the p_i and C_j presumably would be known with high precision relative to other applications. The usual assumption in tagging theory would apply in making inferences about untagged fish.

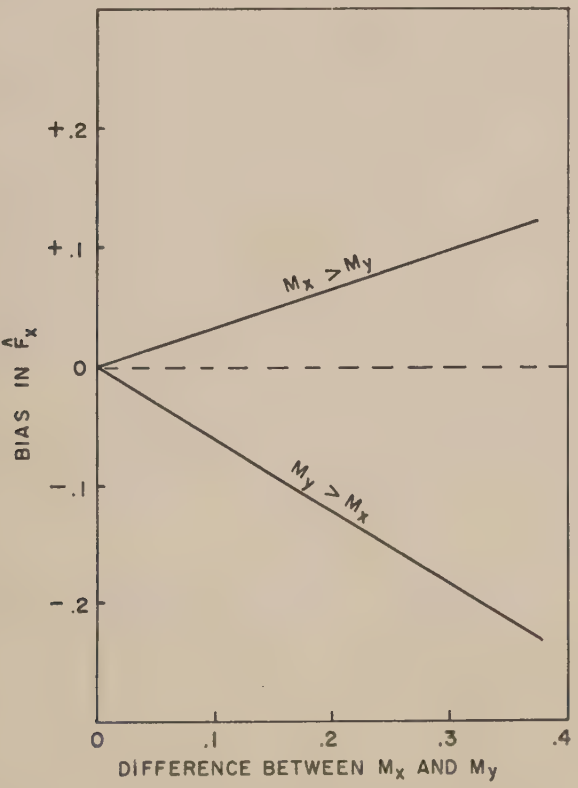

FIG. 1. Bias in estimate of fishing rate for X population when $F_x = 0.6$ and $F_y = 0.2$.

The case of a known final population is admittedly unique. Yet we do find size-selective fisheries on anadromous species whose growth is negligible in the catch interval and whose spawners are counted or estimated. In the Pacific salmons (*Oncorhynchus* spp.), for instance, p_2 as measured on the spawning grounds may be less than p_1 as measured in the river or estuarine fishery; actual causes of the estimated natural mortality, as from dams, may be of particular interest in such applications. Other applications may be to inland species:

where counts of poisoned fish are made at the end of an angling season on lakes or streams, or where water is drawn down and fish stranded.

In common with other methods of estimating fishing rates, the change-in-composition method may suffer most from inexact knowledge of availability and from the difficulty of getting representative samples. Yet continuing interest in methods of assessing important parameters of fish populations, and particularly the fact that catch is accessible to thorough study, suggest that the simple principles involved may find future application.

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SURVIVAL AND MOVEMENTS OF THE FLATWORM, STYLOCHUS ELLIPTICUS, IN DIFFERENT SALINITIES AND TEMPERATURES

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The flatworm, *Stylochus ellipticus,* an experimentally-proven predator of oysters (Loosanoff, 1956), is one of the most abundant marine polyclads along the Atlantic and Gulf coasts of the United States (Hyman, 1940) and, consequently, may be one of the most important oyster enemies. A review of the literature offered by Hopkins (1949, 1950) showed that there is little published information regarding its physiological behavior. However, Pearse and Wharton (1938) in their report on the physiology of the related species, *Stylochus inimicus,* from Apalachicola Bay, Florida, included some observations on *Eustylochus meridionalis* (*Stylochus ellipticus*) from the same area. They found that *S. ellipticus* could survive a slow decrease in salinity from 32 parts per thousand to as low as 2.9 ppt, but died in salinities below 6 ppt if the decrease was abrupt. They also reported that the worms became dormant at temperatures below 7° C. These circumstances suggested that some environmental control of *S. ellipticus* might exist in certain areas in cold climates, especially where low salinity and low temperature coincide.

Since information on the physiological behavior of *S. ellipticus* in the northern part of its range is lacking, our studies were initiated to observe the behavior of adult worms (10 to 18 millimeters long) of Milford Harbor, Connecticut, at different salinities and temperatures, with emphasis on observations at low temperatures and salinities. While the salinity of Long Island Sound proper usually fluctuates within a narrow range of approximately 26 to 28 ppt, oyster beds located in estuaries, salt water ponds and rivers may at times, especially in the early spring, be exposed to water that is almost fresh. The annual range of water temperature in this latitude is from about − 1° C. to approximately 25° C.

Effects of salinity

Observations were made on survival of the worms in different salinities and the effect of these salinities on movement of these worms. "Righting time," *i.e.,* the time required for a worm to return to normal position after having been turned ventral side up, was used as a quantitative measure. Righting times were determined frequently at each salinity tested; however, more observations were made at the lower salinities, where individual variations in righting time were largest, than at the higher salinities. All observations were made in the laboratory at room temperature (18° C. to 22° C.) in standing water, which was changed twice a week. The low salinities were made by diluting sea water from Milford Harbor (about 27 ppt) with tap water demineralized by a Barnstead BD-2 apparatus.

In the first experiment the effects of an abrupt decrease in salinity on survival and righting time of *S. ellipticus* were investigated. Groups of 10 worms each were transferred directly from Milford Harbor water to enamel pans, arranged in pairs,

each containing six liters of water of the following salinities: 25, 22.5, 20, 17.5, 15, 12.5, 10, 7.5, 5 and 2.5 ppt and fresh water. Two groups, each containing 10 worms placed in undiluted water from Milford Harbor, served as controls.

Worms transferred directly to salinities as low as 7.5 ppt survived this abrupt change. Those transferred to salinities of 10 ppt showed no distress at any time,

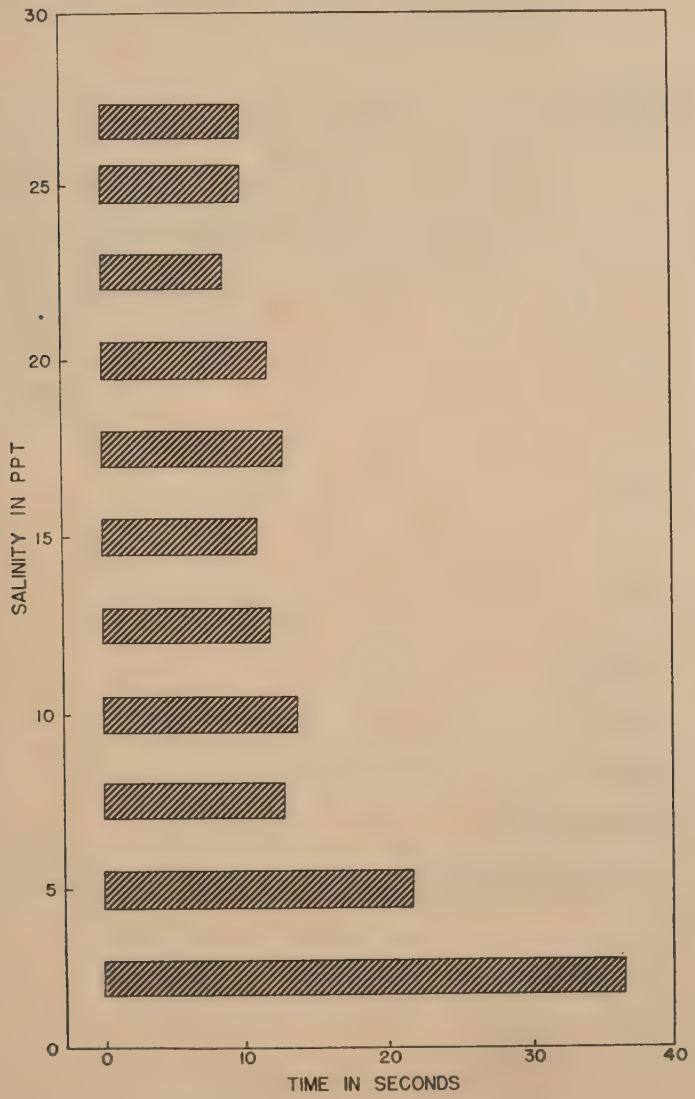

FIGURE 1. Average righting time of *Stylochus ellipticus* from Milford Harbor, Conn. in different salinities at room temperature (18°–22° C.).

while in a salinity of 7.5 ppt some worms, during the first two days, lost color, secreted slightly more mucus than is normal and were sluggish. The worms transferred to 5 ppt were similarly affected, but for a longer time. Four of these died during the first week after transfer, but the survivors eventually ceased to show symptoms of distress and assumed a normal appearance. All of the worms transferred directly to 2.5 ppt and fresh water died within a few hours. However, when some that had become acclimated to a salinity of 5 ppt were transferred to 2.5 ppt, they showed no signs of distress and remained alive and active.

After all symptoms of distress had disappeared in the low salinities, righting times were determined for worms of all groups. The average righting time ranged from 10 to 13 seconds in all salinities, except 5 ppt and 2.5 ppt. In 5 ppt it was 22 seconds and increased to 37 seconds in 2.5 ppt (Fig. 1).

In a second experiment, survival of worms in salinities below 5 ppt was determined after they had been conditioned at intermediate salinities. Three groups of 100 worms each were conditioned for two weeks; one group, at a salinity of 15 ppt;

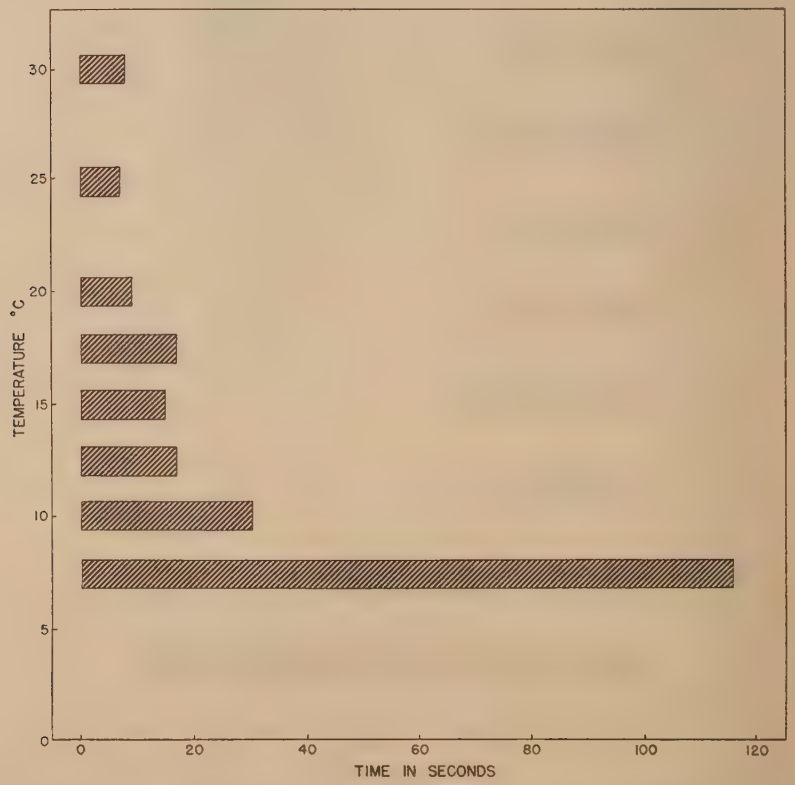

FIGURE 2. Average righting time of *Stylochus ellipticus* from Milford Harbor, Conn., at different temperatures in a salinity of about 27 ppt.

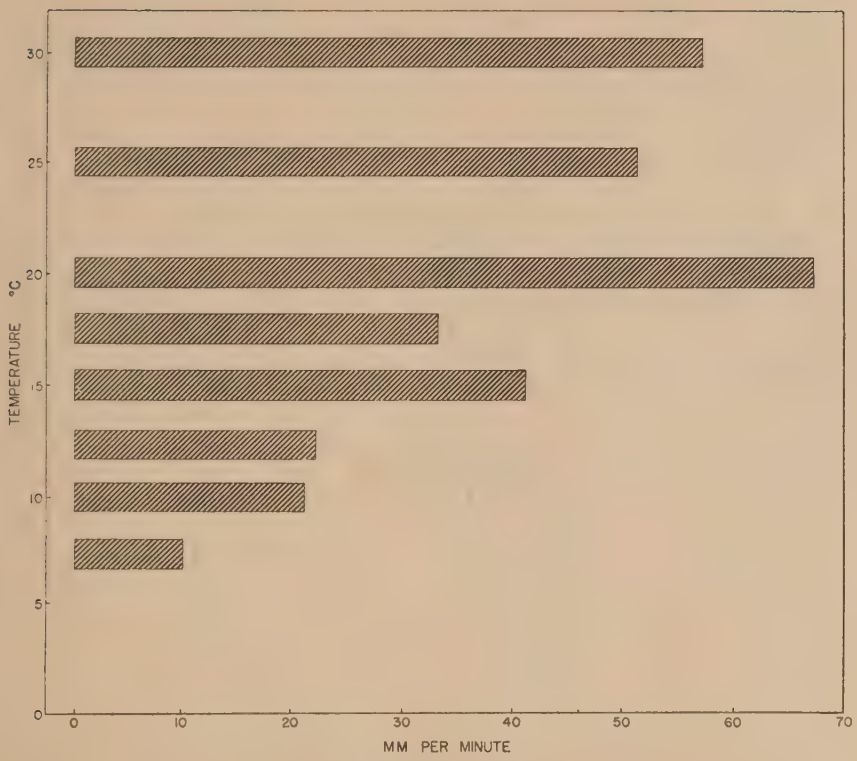

FIGURE. 3. Average locomotion rate of *Stylochus ellipticus* from Milford Harbor, Conn., at different temperatures in a salinity of about 27 ppt.

another group, at 10 ppt; and the third, at 5 ppt. Early in the conditioning period 16 of the worms in 5 ppt died, but the remainder of this group became acclimated. None of the worms died or showed distress in either 15 ppt or 10 ppt. At the end of the two weeks of conditioning, groups of ten worms from each conditioning salinity were placed in duplicate enamel pans, each containing six liters of standing water of the following salinities: 2.5, 1.5 and 0.5 ppt and fresh water. Two groups of ten worms each, placed in undiluted Milford Harbor water, served as controls.

Conditioning at intermediate dilutions had little effect on the ability of these worms to survive in low salinities. By the end of the fourth day all the worms conditioned for two weeks at 15 ppt and then transferred to salinities of 2.5 ppt and lower had died. Worms conditioned at 10 ppt had died by the end of the seventh day after transfer. Those conditioned at 5 ppt, and transferred to 1.5 ppt and 0.5 ppt and fresh water, also were dead by the end of the seventh day. Twelve of the 20 worms conditioned at 5 ppt and transferred to 2.5 ppt died by the end of the seventh day, but the remaining eight were alive and healthy when the experiment ended. Only one of 20 worms in the control pans died during the experiment.

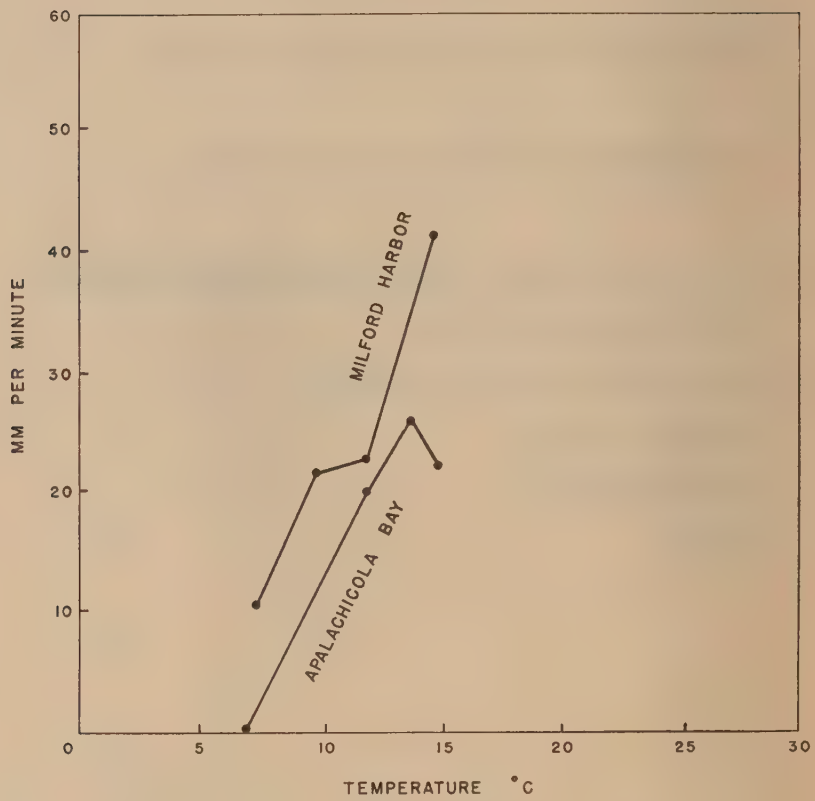

FIGURE 4. Average locomotion rates of *Stylochus ellipticus* from Milford Harbor, Conn., and from Apalachicola Bay, Florida at similar water temperatures.

Apparently, the lowest salinity in which *S. ellipticus* of Milford Harbor can survive, even with prior conditioning at an intermediate salinity, is about 2.5 ppt.

Effects of temperature

The effects of temperature on righting time and "locomotion rate," *i.e.*, the rate of forward movement, of *S. ellipticus* were observed in running sea water at 30°, 25°, 20°, 17.5°, 15°, 12.5°, 10° and 7.5° C. The water temperatures were maintained within ± 1° C. of the desired levels by mixing, in different proportions, heated and unheated Milford Harbor water.

Three groups of ten worms each were allowed to adjust to a selected temperature for three days. Within the next week three separate observations were made on righting time and locomotion rate of all of the worms. At the end of this time the water temperature was changed, the worms were allowed to adjust to the new temperature, and a new series of observations was made. Locomotion rate was

determined by noting the length of time needed for each worm to move 40 mm., without stopping, in a straight line.

The average righting time at 20°, 25° and 30° C. was fairly constant at 7 to 9 seconds, but increased to 17 seconds at 17.5° C. and remained at approximately this level at temperatures down to and including 12.5° C. At 10° C. righting time increased to 30 seconds and rose sharply to 116 seconds at 7.5° C. (Fig. 2).

The average locomotion rate varied somewhat erratically at different temperatures, but tended to decrease with decreasing temperature. From a rate of over 50 millimeters per minute at 20° C. and higher it dropped to approximately 10 mm./min. at 7.5° C. (Fig. 3). A comparison of average locomotion rates observed in this experiment with similar data reported by Pearse and Wharton (1938) for *S. ellipticus* from Apalachicola Bay showed that, at the same temperatures locomotion rates of Milford Harbor worms were consistently higher than those of Florida worms (Fig. 4). This difference may indicate the existence of physiological races within this species of flatworm.

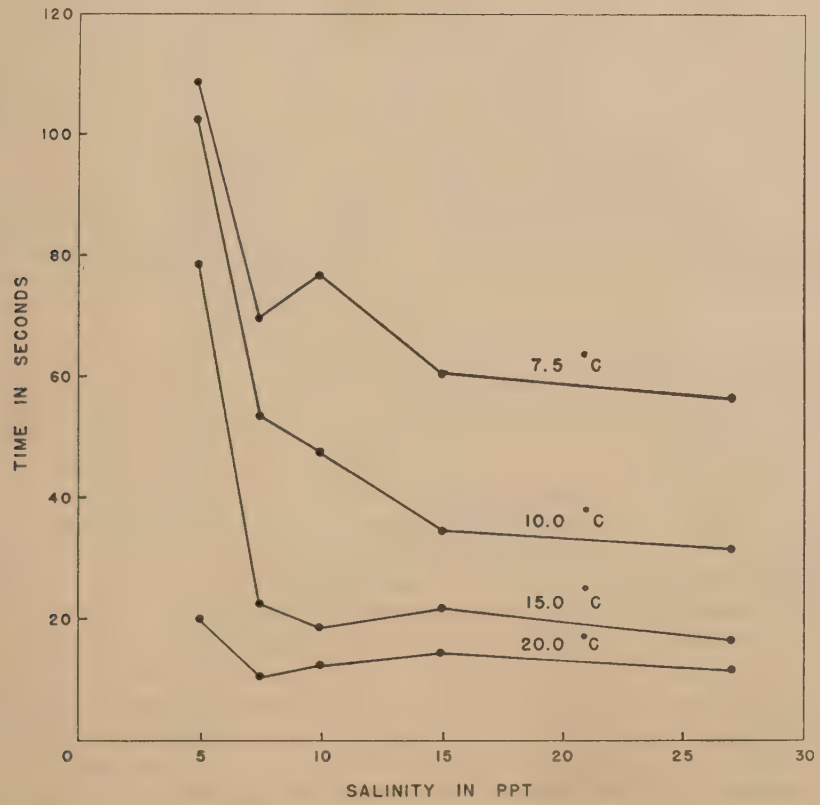

FIGURE 5. Average righting time of *Stylochus ellipticus* from Milford Harbor, Conn. at different salinities and temperatures.

Combined effects of temperature and salinity

The combined effects of temperature and salinity on survival and movement of *S. ellipticus* were also studied. Again, righting time was used as a criterion of movement. Duplicate groups of five worms each were held in polyethylene boxes in three liters of standing water of different salinities. These boxes were kept in a water bath where the desired temperatures were maintained.

The procedure used to study the combined effects of temperature and salinity on the righting times of worms was similar to that used in observing the effect of temperature alone, *i.e.,* worms in all salinities were held at the same temperature until their righting times had been determined, then the water temperature was changed and the observations repeated. Using this procedure righting times were obtained in Milford Harbor water at a salinity of about 27 ppt and also in salinities of 15, 10, 7.5 and 5 ppt at temperatures of 20°, 15°, 10° and 7.5° C. Worms tested at 5 ppt were conditioned to this salinity prior to starting the experiment.

Although worms showed some movement in all combinations of temperature and salinity tested, the effects of low temperature and salinity in slowing down their movements became more apparent as the two factors were progressively lowered, and the depressing effects of each factor on their movement tended to reinforce one another (Fig. 5). For example, at 20° C. worms in all salinities from Milford Harbor water to that of 7.5 ppt had approximately the same average righting time, ranging from 11 to 15 seconds, but worms in 5 ppt required an average of 21 seconds to turn over, reflecting primarily the adverse effect of low salinity.

At 15° C. the average righting times of worms in 7.5 ppt and higher salinities were again about equal, but had increased slightly to approximately 18 seconds, due to the effect of the lower temperature. In 5 ppt, however, righting time increased more sharply than expected. For example, at normal salinity a decrease in temperature to 15° C. had no appreciable effect on righting time, and at room temperature lowering of the salinity to 5 ppt had only increased righting time to 22 seconds, but when the temperature was reduced to 15° C. and the salinity to 5 ppt, simultaneously, righting time increased to 79 seconds. The combined effect was, therefore, greater than could have been predicted from the effects of these factors when studied separately.

At 10° C. worms in all salinities were affected by lowered temperature, while those in salinities of 5, 7.5 and 10 ppt showed the exaggerated effect of a combination of low temperature and salinity. For example, in Milford Harbor water and in 15 ppt the average righting time was 32 and 35 seconds, respectively, while at 10 ppt it was 48 seconds, 54 seconds at 7.5 ppt and 103 seconds at 5 ppt.

At a temperature of 7.5° C. the worms in all salinities had slowed their movements still further, but the same pattern of increase in righting times was noted.

In many areas where oyster cultivation is carried on, pronounced variations occur in either temperature or salinity or both. If the rate of predation of flatworms on oysters is closely related to the worms' ability to move about, our studies indicate that predation by these worms must vary considerably at different seasons of the year, especially in a cold climate. Even though their predatory activities may be curtailed by low temperature or low salinity, their ability to survive these adverse conditions makes them a serious threat wherever oyster culture is practiced.

We wish to express our appreciation to Dr. V. L. Loosanoff for suggesting this problem and for his critical review of the manuscript. We also wish to thank Mr. Harry C. Davis for his helpful suggestions in the preparation of this paper, Mr. Manton Botsford for the illustrations and Miss Rita Riccio for her careful editing.

Summary

1. *Stylochus ellipticus* from Milford Harbor, Connecticut, survived abrupt transfer from a salinity of about 27 ppt to salinities as low as 7.5 ppt at room temperature. Those transferred directly to 5 ppt suffered a mortality of 20% but all worms died when placed directly in 2.5 ppt and fresh water. However, worms that acclimated to 5 ppt survived subsequent transfer to 2.5 ppt.

2. Righting time of *S. ellipticus* at room temperature remained constant at 12 to 15 seconds in salinities ranging from about 27 ppt to 7.5 ppt but increased to 22 seconds in 5 ppt and to 37 seconds in 2.5 ppt.

3. Righting time of *S. ellipticus* in a salinity of about 27 ppt was approximately 8 seconds at temperatures of 20°, 25° and 30° C., 16 seconds at 12.5°, 15° and 17.5° C., 30 seconds at 10° C. and 116 seconds at 7.5° C.

4. Locomotion rate of *S. ellipticus* varied erratically with temperature but generally decreased with temperature decreases below 20° C. It exceeded 50 millimeters per minute at temperatures of 20° C. and higher but decreased to 10 mm./min. at 7.5° C.

5. At the same temperatures *S. ellipticus* from Milford Harbor moved faster than reported for the same species from Apalachicola Bay, Florida. This observation suggests that there may be physiological races within this species of flatworm.

6. When temperature and salinity were lowered simultaneously righting time of *S. ellipticus* was frequently longer than the combined righting times obtained when the two factors were observed separately.

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Efficiency and Rate of Yolk Utilization by Developing Embryos and Larvae of the Pacific Sardine *Sardinops caerulea* (Girard)[1]

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ABSTRACT

The chemical composition of ripe Pacific sardine ovaries, composed primarily of yolk, is almost identical to that of yolk extracted from planktonic sardine embryos and larvae. Caloric measurements were made on ripe ovaries and the values obtained were used to estimate the caloric content of individual sardine embryos and larvae.

Water content of sardine egg and larval yolk averages 91.2%. An egg with a yolk volume of 0.56-mm³ has a caloric reserve of 0.30 calorie when spawned. Caloric uptake from the embryonic and larval yolk was measured against time, and caloric utilization due to catabolic processes was analysed by indirect calorimetry (oxygen consumption) with changing embryological development and swimming activity. The caloric value of the remaining yolk 160 hours after spawning (at 14°C) is not sufficient to completely support the sardine larva's catabolic processes. This deficit is made up by resorption of tissue and is reflected in a loss of larval weight. Yolk is converted into tissue with an average assimilation coefficient of about 79%.

INTRODUCTION

Most pelagic fish larvae do not feed when hatched but have a yolk supply that provides their nutritional needs for growth and metabolism until feeding begins. Analyses of larval yolk afford an opportunity to study a food supply presumably ideally adapted to the metabolic requirements of the fish. Very little information has been available on the efficiency and rate that yolk can be utilized by embryos and larvae of pelagic fishes. This study presents such information for the pelagic embryo and yolk-sac larva of the Pacific sardine, *Sardinops caerulea* (Girard).

METHODS AND MATERIALS

The developing, pelagic egg of the Pacific sardine is approximately 1.7 mm in diameter (Ahlstrom, 1943) with a spherical yolk of about 1 mm in diameter enclosed in a subchorionic (perivitelline) space filled with sea water (Lasker and Theilacker, 1962a) and surrounded by a thin, turgid outer membrane, the chorion. An oil droplet, 0.2 mm in diameter, is oriented at the vegetal pole of the yolk sphere and the embryo initially develops at the opposite pole. At hatching, the sardine larva has not completed its embryological development and lacks a mouth, gills, and an open intestinal tract.

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Observations were made on ripe sardine ovaries to compare with those made on larvae. Maximum ovum diameters were measured for each ovary, and only those having eggs with diameters of 0.6 mm or greater and containing yolk uniformly distributed throughout, were considered ripe (MacGregor, 1957). Unlike other clupeids, e.g. the herring *Clupea harengus* (Blaxter, 1956), the female Pacific sardine is rarely taken in a running-ripe condition. This may be due to the short time interval, probably measured in hours, in which the already mature but opaque eggs imbibe or absorb water, become translucent, and are spawned.

The measurements described here were performed on fertilized sardine eggs and the larvae hatched from these eggs in laboratory jars. The developing eggs were taken in surface plankton hauls in the Pacific ocean off San Diego, California, at temperatures ranging from 14.2 to 17.0°C. The jars containing eggs were kept in a styrifoam insulated box until brought back to the laboratory where they were maintained at 14°C.

Respiratory measurements of individual sardine embryos and larvae were made with the reference diver technique described by Scholander *et al.* (1952). Results are given as oxygen consumed in microliters per single egg or larva per hour (QO_2). The factors affecting the magnitude of respiration are discussed in an earlier paper (Lasker and Theilacker, 1962a). The method of extracting yolk from individual larvae was described earlier (Lasker and Theilacker, 1962a). Water content and percent dry weight were obtained by drying yolk at 75°C in pre-weighed capillary tubes to a constant weight. Weighings were made with an electrobalance to ±0.001 mg (Cahn Instrument Co., Paramount, California). Single larvae were weighed with this balance after rinsing them briefly in distilled water and by drying on small pre-weighed pieces of aluminum foil.

Embryonic and larval yolk volumes were calculated from photographs of eggs and larvae taken at intervals during the yolk consumption period. Intra-ovarian ovum diameters were measured by MacGregor's method (1957).

Total nitrogen (N) was determined by the standard micro-Kjeldahl procedure employing a Kirk still (Kirk, 1936) after sulfuric acid digestion with a selenized Hengar granule as a catalyst. Protein was calculated from the relationship N × 6.25 (Hawk *et al.*, 1954). Non-protein nitrogen of homogenized ovaries was determined after precipitation of protein with 10% trichloracetic acid and a Kjeldahl determination performed on the supernatant fluid.

Water in ovaries was determined by drying the tissue in a vacuum oven at 75°C to a constant weight. Other chemical measurements were made using the following techniques: carbohydrate (Somogyi, 1952); total lipid and phospholipid (Colowick and Kaplan, 1957; Bartlett, 1959). Ash was determined by combusting the dry ovary at 500°C and weighing the residue.

Caloric measurements were made with a bomb calorimeter utilizing a semi-micro oxygen bomb (Parr Instrument Co., Moline, Illinois) after freeze-drying the tissue to be analyzed.

RESULTS

A knowledge of the degree of yolk dilution is necessary if accurate estimates are to be made of the organic material available to the larva from volume measurements of the yolk. Table 1 presents analyses of water content for 10 individual larval yolks. This shows there is little variation in water content from larva to larva. The water content of larval sardine yolk averages 91.2% as compared with the average of 70.7% found in ripe ovaries (Table I). I was fortunate in obtaining two running-ripe females whose eggs were exuding from the genital pore. Unlike the ova from the other ovaries examined, these ova were 1.2 mm in diameter, had translucent and swollen yolk, and the fat had separated into the discrete droplet characteristic of the planktonic egg. Both of these ovaries had over 88% water.

TABLE I. Analytical results. Mean values are followed by the standard deviation and (in brackets) the number of replicates. Yolk was obtained from spawned eggs. Ripe ovaries had maximum ovum diameters ranging from 0.6 to 1.0 mm.

	Larval yolk	Ripe ovaries
Percent water	91.2±1.4 (10)	70.7±1.5 (10)
Percent Total N, of dry weight	11.4 (2)	11.5±0.6 (10)
Percent protein, of dry weight (N × 6.25)	71.3	71.6
Percent fat, of dry weight	...	13.0±1.5 (11)
Calories per gram dry weight (bomb calorimeter)	...	5386±194 (9)

Protein is the chief yolk constituent in fishes (Smith, 1957), and amounts to over 70% of the yolk dry weight in the sardine. Because the yolk available from individual larvae was so small (<1 μl from each), analyses for caloric content had to be made on ripe ovaries; this was justified because their organic composition was almost identical. Analyses for total N showed that larval yolk and ripe ovaries have similar nitrogen content and that their protein electrophoretic patterns are indistinguishable, due to the fact that ripe ovary is composed almost wholly of ova containing yolk.

Phospholipids constituted approximately 11% of the dry weight of sardine eggs (range for 6 determinations, 8.2–12.5%). Glyceride fat was 4% of the total dry weight as calculated from the volume of the droplet and the specific gravity of sardine oil (Bailey, 1952). The qualitative and relative quantitative composition of the constituent fatty acids comprising the lipids found in spawned eggs was found to be identical to that of ripe ovary lipids (Lasker and Theilacker, 1962b). However, the variations in total fat recorded for ripe ovaries (Table I) may account for the slight differences found in caloric measurements between ovaries. The fat content of 16 ripe ovaries averaged 13.0%.

Tests for reducing substances before and after hydrolysis of sardine ovaries showed that there is less than 1% carbohydrate in dry ovarian tissue. Non-protein nitrogen was similarly low, averaging 0.7%. Ash averaged about 7%.

The contribution of these organic and inorganic substances to the caloric value of sardine ovaries is negligible.

The similarity in quality and quantity of the major organic constituents in ripe ovarian tissue and larval yolk justifies caloric measurements of ripe ovaries to be applied to larval yolk. The caloric content of sardine ovarian yolk was found to average 5386 calories per gram dry weight.

Lasker and Theilacker (1962a) have shown that swimming and embryonic development are the two major factors influencing oxygen consumption in embryonic and larval sardines provided that temperature is constant. The average rates and their standard deviations for oxygen consumption by 33 individual embryos and larvae over the yolk-sac period are presented in Table II. By summing the mean rates over each time interval an overall sum of

TABLE II. Average oxygen consumption at 14°C by sardine embryos and larvae.

Number of animals	Time	QO_2	Standard deviation
7	0–42 hours	0.030	±0.0098
9	42–70 hours	0.066	±0.010
17	70–180 hours	0.088	±0.019

microliters of oxygen consumed per animal per 180-hour yolk-sac period is obtained. The caloric value of oxygen varies 7% for the full range of respiratory quotients associated with the utilization of protein, fat and carbohydrate (Swift and French, 1954), or 4690 to 5050 calories per liter of O_2 for R.Q.'s of 0.707 to 1.00. Therefore, 1 μl O_2 = 0.005 cal ±0.00035 cal, and the sardine embryo utilizes 0.063±0.0044 calories for catabolism during a 180-hour yolk-sac period.

In Table III the catabolic requirements of sardine embryos and larvae are presented as they change with time. Yolk uptake is plotted as a volume decrease

TABLE III. Average yolk utilization by sardine embryos and larvae at 14°C expressed as diminishing volume and caloric uptake. The catabolic calories are based on the mean respiratory figures given in Table II. A calculation for percentage efficiency of yolk conversion to tissue is included below.

Elapsed hours from spawning	Yolk volume (mm^3)	Calories remaining	Catabolic calories
0	0.56	0.300	0
42	0.48	0.260	0.0063
71	0.29	0.160	0.0096
80	0.25	0.130	0.0040
100	0.16	0.085	0.0088
120	0.09	0.048	0.0088
140	0.04	0.021	0.0088
160	0.01	0.005	0.0088
180	0	0	0.0088
			Total = 0.064

$$\text{Percentage efficiency} = 100 \times \frac{0.300-0.064}{0.30} = 78.7\%$$

in Fig. 1 and presented as caloric utilization in Table III. No eggs were taken at precisely the time they were spawned, but at 20 hours after spawning there had been very little embryonic development and yolk uptake (Ahlstrom, 1943). It is assumed therefore that the volumes at 20 hours do not differ significantly from those at spawning. After this time the yolk is used at a rapid rate until it is finally completely consumed. It can be seen in Table III that the larvae have enough yolk during almost the entire yolk-sac period to provide for both catabolism and anabolism. After 160 hours there is only enough yolk to provide for somewhat less than is needed for respiratory requirements, and during this period the animal is on a deficit. This deficit appears to be made up by resorption of tissue.

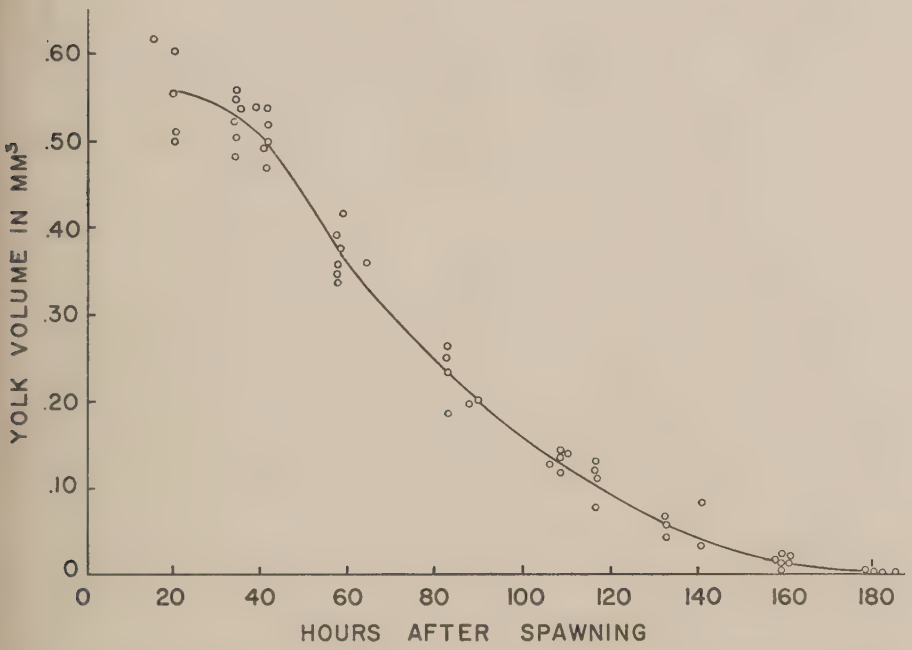

FIG. 1. Change in larval sardine yolk volume with time at 14°C. Each dot represents a different larva. Hatching occurred at 78 hours after spawning. The curve is plotted through average values at each time interval.

The gravimetric determinations of individual larval sardine weights with time are given in Fig. 2. Weight loss does not become evident until about 240 hours post-spawning. A line indicating the calculated average weight loss with time (0.081 microgram/larva/hour) is superimposed on the individual larval weights. There is a reasonably good agreement between the observed weights and the calculated weights after the larvae are 240 hours old. The weights plotted from 80 hours through 200 hours do not follow the projected slope closely. This is probably due to the variability of individual larvae in their swimming

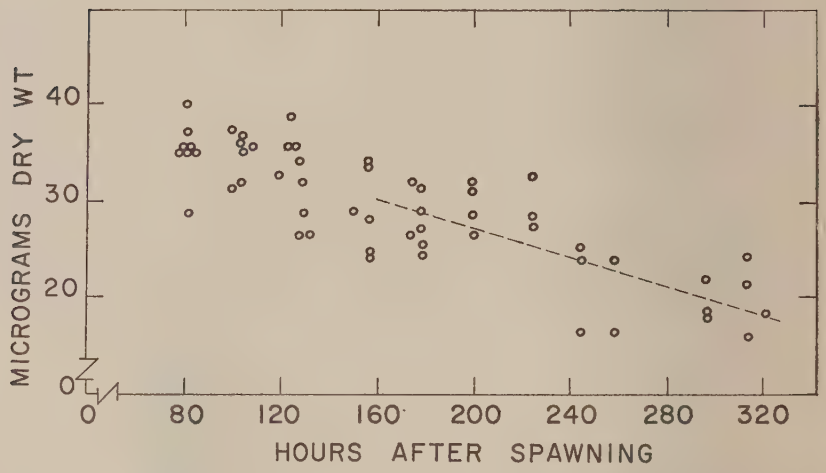

FIG. 2. Dry weights of individual sardine larvae after hatching. The oblique line represents the calculated weight loss due to catabolism.

activity. Larvae swimming actively and for sustained periods would catabolize and lose weight at a higher than average rate. Quiescent larvae would resorb less tissue per unit time.

Catabolism accounted for by respiration amounts to 21% of the caloric requirement over the entire yolk-sac period when calculated on the basis of 0.56 mm^3 yolk volume. The remainder (79%) is that which goes into the growth of the larva and the fraction due to excreted nitrogenous materials. Ivlev (1939) showed that the energy of waste products produced during the yolk-sac stage of the sheatfish, *Silurus glanis*, is very small, amounting to only 2% of the total energy available in the yolk. I analyzed for total nitrogen sardine eggs and larvae approximately 20 and 100 hours after spawning, respectively (Table IV). The loss of nitrogen due to excretion is so small that it could not be detected by the method used. Loss in energy due to excretion appears to be of the same order of magnitude as reported by Ivlev. For the smallest initial yolk volume measured, 0.50 mm^3, 23% would go for catabolism and 77% into growth. Smith (1947, 1952, 1957) and Hollett and Hayes (1946) found respectively a 60.2% efficiency for the trout (*Salmo irideus*) and 41% for the Atlantic salmon (*Salmo salar*) during development, by calculating from chemical analyses of the yolk using standard conversion factors for protein, fat and carbohydrate. Ivlev (1939) calculated an overall efficiency of 66% for the yolk-sac stage of the sheatfish.

TABLE IV. Total nitrogen of Pacific sardine eggs and larvae.

Number of eggs or larvae	Hours after spawning	Wt. total N (mg)	N per egg or larva
201 eggs	20	0.801	0.00399
389 larvae	100	1.567	0.00403

DISCUSSION

In this paper the quantitative energetic relationship of yolk to the developing sardine embryo and larva has been determined. Chemical analyses of the yolk confirm, in general, what is known of the chemistry of other teleost egg yolks (Smith, 1957), i.e., that protein is the most important food reserve, lipids also contribute a large part of the energy available to the embryo, and carbohydrates are of lesser importance as energy reserves. It has been shown that sardine larvae begin to show signs of tissue resorption and subsequent weight loss after the yolk has been completely consumed. This is probably due to the continued catabolic activity of the animal when no food is available. Berner (1959) and Arthur (MS, 1956) have noticed respectively that most of the anchovy (*Engraulis mordax*) and Pacific sardine larvae obtained from plankton hauls are in poor condition and have resorbed their livers. Shrinkage of starving sardine larvae after yolk-sac absorption is evident from Farris's (1959) data. By examining gut contents of Pacific sardine larvae caught in plankton nets, Arthur (1956) concluded that feeding incidence is very low, rarely exceeding 15% and generally below 10%. These facts indicate that many sardine larvae are starving in nature.

Laboratory observations of the developing larval sardine indicate that the jaw is not functional when the animal begins its metabolic deficit, i.e. the time that catabolism exceeds the energy provided by the remaining yolk supply. At the same time the larva's eyes are not fully pigmented, and lack of vision also must be a problem. Active seeking and capture of food probably does not begin until a later, as yet undetermined, time. Thus, at 14°C yolk utilization proceeds for 160 hours, and all of the metabolic requirements of the developing larva are met. The jaw starts forming at this time, but the animal does not have enough yolk to meet its metabolic requirements and goes on a partial deficit until 180 hours. By this time the yolk is completely utilized, and the jaw has developed fully. The larva swims actively at this age but does not appear to pursue moving nauplii or other food particles. If the animal does not come upon a particle of food by chance to overcome its continuing metabolic deficit, it will die shortly after vital physiological functions are affected. Increased temperature would undoubtedly have an accelerating effect on this process.

SUMMARY

1. Chemical analysis of Pacific sardine (*Sardinops caerulea* Girard) ripe ovaries which are composed chiefly of yolk, shows that protein is the major nutrient, amounting to over 70% of the dry weight; lipids constitute about 13%. The average caloric value of the ripe ovary is 5386 calories per gram dry weight.

2. Chemical analysis of larval yolk gave similar qualitative and quantitative results as those obtained with ripe ovaries. Thus caloric values obtained with ripe ovaries can be used to describe changes occurring while yolk is being utilized by the larva.

3. The caloric content of a single 0.56 mm^3 sardine egg yolk, based on an average water content of 91.2%, is 0.30 calorie.

4. Yolk volume changes with time in the embryo and larva indicates that the calories provided by the yolk meet the metabolic needs of the animal at 14°C until 160 hours after spawning. From this time on the larva is on a continuing energy deficit.

5. Although the jaw begins to form at about 160 hours, it is not fully formed until 180 hours after spawning. The larva does not actively pursue food available to it in laboratory jars. Although larvae of this age can swim actively the pursuit and grasping of food does not appear to be developed as yet. Hence obtaining food may simply be a matter of chance meeting between mouth and food particle.

6. If the energy deficit continues, as in a starving larva, concomitant weight losses occur due to tissue resorption which finally result in death.

7. For the volume of yolk (0.5–0.6 mm^3) available to sardine embryos, the efficiency of yolk utilization (i.e. conversion of yolk to tissue) for the entire yolk-sac period ranges from 77 to 79%. Energy loss due to excretion of waste products is small and could not be measured with available techniques.

I wish to acknowledge the technical assistance of Mrs Gail Theilacker and Mr Gerald Sanger.

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REUBEN LASKER and GAIL H. THEILACKER

OXYGEN CONSUMPTION AND OSMOREGULATION BY SINGLE PACIFIC SARDINE EGGS AND LARVAE (*SARDINOPS CAERULEA* GIRARD)

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Oxygen Consumption and Osmoregulation by Single Pacific Sardine Eggs and Larvae (*Sardinops caerulea* Girard)

By

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Introduction

The respiratory rates of planktonic marine fish eggs and larvae are of considerable interest in that they permit assessment of energy requirements. Yet oxygen consumption measurements of planktonic fish eggs or larvae have been confined to very few species, e.g. the plaice (BURFIELD, 1928). Demersal fish eggs have been studied by a few workers (HYMAN, 1924; AMBERSON and ARMSTRONG, 1933) but fish larvae have been neglected. In early studies many eggs were measured at the same time because the methods used lacked sufficient sensitivity to measure the oxygen consumption of single eggs.

This report presents data on oxygen consumption of single Pacific sardine eggs and larvae measured with the sensitive reference diver technique devised and described by SCHOLANDER, CLAFF, and SVEINSSON (1952). This method permits observation of a single egg or larva while oxygen consumption is measured. Thus changes in heart beat, swimming activity, development and time of hatching can be correlated with oxygen uptake.

It was also of interest to determine whether salinity stresses of larvae and eggs could be detected by concomitant changes in rate of oxygen consumption. We were able to compare oxygen consumption of eggs and larvae in different salinities only in a few experiments because in most of our attempts the swimming activity of a larva or twisting movements of an embryo increased metabolism in excess of the differences we were trying to measure.

Finally, efforts have been made to ascertain the extent to which sardine eggs and larvae need to regulate their salt balance in sea water and whether they could tolerate experimentally induced salinity stresses. Data are presented here intended to elucidate these points.

Methods

Fertilized sardine eggs were obtained from surface net hauls taken at various times throughout the year off the coast in the vicinity of San Diego. The developmental stage of the embryo varied depending on the time after being spawned at which they were caught. In order to minimize temperature fluctuations during transportation, the eggs were kept in litre jars of sea water in a styrifoam-insulated box. Eggs were caught at temperatures ranging from 14·2 to 17·0°C and were kept in the laboratory at 14 $\pm$ 1°C.

The reference diver technique (SCHOLANDER, *et al.*, 1952) employed for measuring oxygen consumption has a sensitivity of $\pm 7 \times 10^{-4}$ microlitres. Any activity of the embryo or larva was noted along with oxygen consumption. Constancy of the heart beat rate was taken as a criterion of a healthy condition as moribund animals showed decreases and irregularities in the heart beat rate. Each experiment on oxygen consumption lasted at least one hour. During the experiments temperature was maintained at 14 $\pm$ 0·01°C. In one series of experiments a Warburg apparatus was used to compare oxygen consumption by grouped eggs with the rates obtained with the reference diver.

After drying for 24 hours at 70°C in a vacuum oven, eggs and larvae were weighed to the nearest microgramme with a Cahn electrobalance (Cahn Instrument Co., Paramount, California, USA).

Osmolar concentrations of larval sardine yolks were measured with a melting point apparatus used by GROSS (1954) and described in detail by GIESE (1957). A small volume (one microlitre or less) of the yolk or other fluid to be analysed was drawn into a Pyrex capillary tube, quickly frozen on a slab of dry ice (solid carbon dioxide) and plunged into brine cooled to −10°C. Standard sodium chloride solutions embracing a wide range of molarities were similarly frozen simultaneously. The time of thawing of each solution in the slowly warming brine bath was recorded and plotted against molarity. Our results were expressed in molarities of sodium chloride.

Larval yolk was used for osmolar measurements because it is believed to be isotonic with the circulating body fluid. Larvae, 3 mm long, were removed from sea water with a large bore pipette and placed on a clean slide. The adhering water was absorbed by a piece of filter paper. The yolk-sac, clearly distinguishable under a dissecting microscope, is easily punctured by a fine Pyrex capillary tube (approximately 0·2 mm inside diameter) permitting the watery yolk to enter the tube by capillarity.

Subchorionic (perivitelline) fluid was obtained from eggs by puncturing the chorion with a capillary tube. Yolks from late stage eggs (Stage XI) were withdrawn as described for hatched larvae except that the chorionic membranes were first stripped away under water to release the unhatched embryos.

Osmolarities of adult sardine plasma and sera were determined for comparison with larval yolk. Blood was obtained by cardiac puncture or by severing the caudal artery. To obtain samples of plasma, clotting was prevented by drawing the blood into heparinized capillary tubes which were then rapidly centrifuged to remove the red cells. Serum was obtained by centrifuging non-heparinized capillary tubes containing clotted blood.

AHLSTROM's (1943) classification of *Sardinops caerulea* developmental stages was used to identify the stages and ages at which respiration was measured. The age of the stage is given in hours after spawning at 14·5°C as calculated by AHLSTROM.

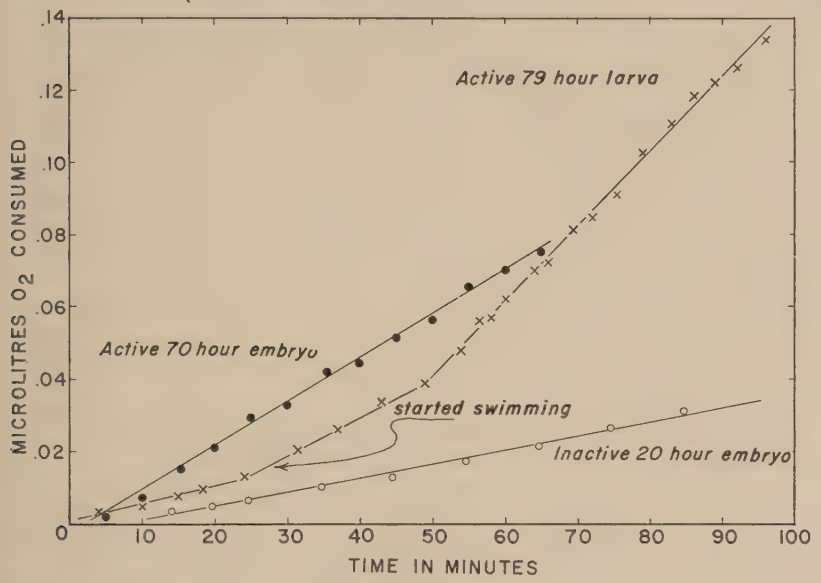

Figure 1. Typical rate curves for oxygen consumption by single sardine eggs and larvae. Q_{O_2}'s in μl/mg dry wt/hr; ○—○, $Q_{O_2} = 0{\cdot}59$; ●—●, $Q_{O_2} = 1{\cdot}90$; ×—×, Q_{O_2} for inactive phase = 1·00, active phase = 3·18.

Results

(a) Oxygen consumption rates of sardine eggs and larvae

Stage of development

The three curves in Figure 1 illustrate the linear relation typical of oxygen consumption by sardine eggs and larvae. From such plots the Q_{O_2} (microlitres of oxygen consumed per milligram dry weight) was determined for each egg or larva studied. There is a general increase in oxygen consumption as the sardine egg develops, this being most evident in quiescent animals. The lowest oxygen uptake was found in the earliest stage we were able to obtain (Stage IV eggs, approximately 20 hours old). The average Q_{O_2} for this early stage was 0·5µl O_2/mg dry wt/hr. The oldest quiescent larvae (190 hours old) had Q_{O_2}'s averaging about 1·7µl O_2/mg dry wt/hr. Data on these and intermediate stages are plotted in Figure 2.

For comparison with our results we have recalculated the data of Hayes, Wilmot, and Livingstone (1951) on Atlantic salmon eggs (*Salmo salar*) and that of Amberson and Armstrong (1933), and Scott and Kellicott (1916) on *Fundulus heteroclitus*. Assuming 75% water content, *S. salar* eggs at 10°C have Q_{O_2}'s of 0·54 and 0·61 at 19 and 50 days old respectively. *F. heteroclitus* eggs and larvae range in Q_{O_2} from 0·14 in early cleavage to 3·9 six days after hatching at approximately 20°C.

Effect of activity

Once the sardine embryo develops sufficient musculature (Stage VIII, 45 hours old) active movements begin. The Q_{O_2}'s of active and quiescent animals

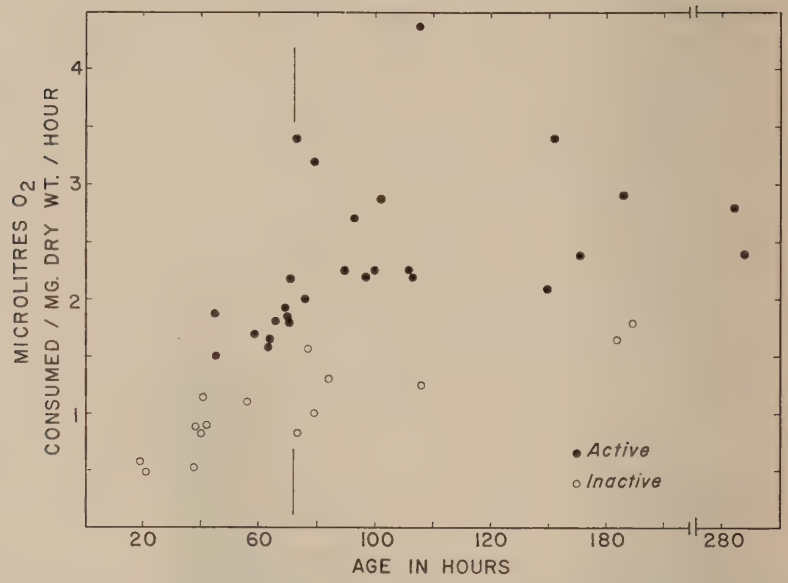

Figure 2. Q_{O_2}'s of active and inactive *S. caerulea* eggs and larvae at 14°C. Vertical line at 72 hours indicates hatching time. Each dot represents an individual egg or larva.

are plotted in Figure 2. Those animals which swam actively consumed 1 to 3 times more oxygen than did quiescent ones. Table 1 compares animals for which we could obtain Q_{O_2}'s in both quiescent and active phases; Table 2 gives the mean values for all organisms tested. No strict correlation could be found between degree of activity and oxygen consumption. Most active animals varied in tail beats from 1 in three minutes to 3 per minute. The highest value ($Q_{O_2} = 4{\cdot}3$) was obtained for a larva which swam continuously during the hour it was observed.

Hatching

Larvae differed in their oxygen consumption immediately after hatching depending on their activity. Twisting movements are general prior to the hatching of a larva from an egg but some larvae become quiescent and use less oxygen after leaving the egg, while others become more active and swim immediately, thereby consuming oxygen more rapidly (Figure 3).

(b) Internal osmotic concentrations and osmoregulation by sardine eggs and larvae

In the developing sardine egg, as in the egg of *Fundulus* (SHANKLIN, 1959), the subchorionic fluid rapidly establishes an equilibrium with the bathing medium. The subchorionic fluids of sardine eggs were compared with sea water in which they were submerged. Five measurements of sea water gave a mean osmolarity of 0·55 M (range: 0·54 — 0·56 M); the subchorionic

Table 1

Increase in oxygen consumption of individual sardine larvae with activity

Q_{O_2}'s in μl/mg dry wt/hr

Number of specimen	Age in hours	Q_{O_2} Inactive	Q_{O_2} Active	Relative increase in O_2 consumption Q_{O_2} active/Q_{O_2} inactive	Comments
1	72–73	0·82	2·18	2·7	inactive as egg active as larva
2	76–77	1·53	1·99	1·3	larva
3	79	1·00	3·18	3·2	larva
4	116	1·25	4·38	3·5	larva
5	186–189	1·78	2·93	1·6	larva

Table 2

Average Q_{O_2}'s and standard deviation for active and inactive *S. caerulea* eggs and larvae

Q_{O_2}'s in μl/mg dry wt/hr

	Number of eggs or larvae	Q_{O_2} Inactive	Number of eggs or larvae	Q_{O_2} Active
Eggs.....	8	0·80 ± ·25	10	1·79 ± ·18
Larvae.....	7	1·33 ± ·36	17	2·68 ± ·63

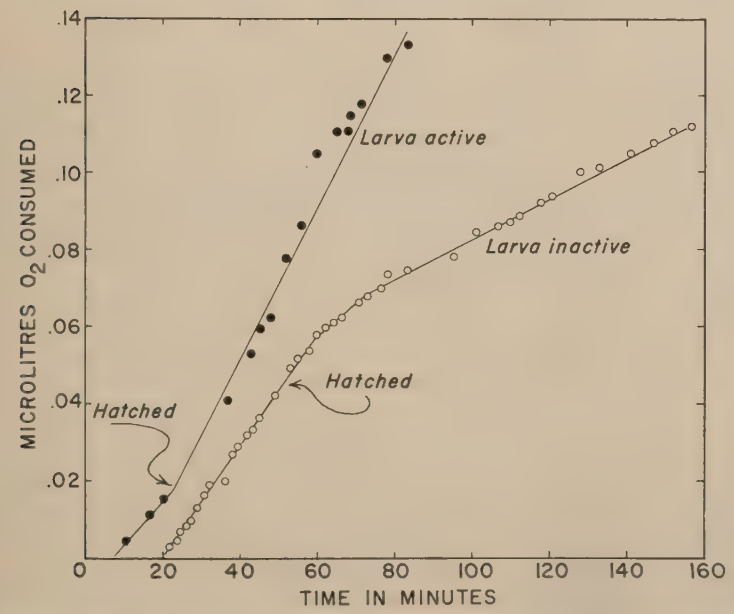

Figure 3. Effect of activity on oxygen consumption of sardine larvae after hatching.

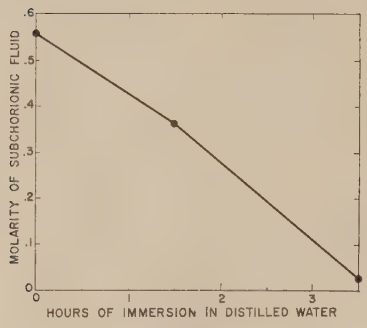

Figure 4. Change in osmolarity of subchorionic fluid of sardine eggs following their transfer from sea water to distilled water. The point at zero hours represents 8 eggs. The other points represent 3 eggs each.

fluids of eight eggs had a mean osmolarity of 0·56 M (range: 0·51 — 0·61 M). Figure 4 shows the drop in molarity of the subchorionic fluid when the eggs are transferred from sea water to distilled water. Within 3½ hours almost all of the dissolved substances in the subchorionic fluid diffuse out. No swelling of the eggs in distilled water was observed while the chorion was intact; however, when the chorion was removed the rapid osmotic inflow of water caused the sac to burst. The subchorionic fluid of an egg in 50% sea water attained the molarity of the medium in about the same length of time as in distilled water.

Table 3 is a compilation of osmolar measurements of the yolks of 34 embryos

Table 3

Osmolar concentrations of yolks of sardine embryos and larvae compared with adult sera and plasma

	Number in sample	Mean molarity	Standard deviation
Yolks of embryos and larvae.	34	0·24	± 0·041
Adult sera and plasma	47	0·19	± 0·027

and larvae ranging from 3·6 to 5·5 mm in length, and of plasma and sera taken from 48 adult fishes 131 to 211 mm in length. The data for eggs and larvae are pooled as are those for adult sera and plasma as they are not statistically different within each group. Sardine embryos and larvae are hypotonic to sea water ($M = 0{\cdot}56$, $S = 35^0/_{00}$) with an average osmolarity of 0·24 M; adult sardine sera and plasma have an average osmolarity of 0·19 M. The difference observed in the mean values between fluids of larvae and adults is significant ($t = 6{\cdot}13$; d. f. $= 79$; $p = < {\cdot}01$) and may be due to large molecular weight protein constituents of the larval yolk.

Sardine larvae were shown capable of withstanding extreme salinity stresses. A number of yolk-sac larvae were put into distilled water two days after hatching and were subsequently removed to determine the internal concentration of each at intervals over a six-hour period. As shown in Figure 5, larvae in distilled water, after an initial loss of salts, maintain a lower than normal internal concentration for some time. Most of the larvae tested lived in this condition for at least 24 hours. One specimen lived for three days; the heart continued to beat but yolk utilization was slowed considerably and a somewhat enlarged yolk-sac sinus appeared. Development was retarded so that the eyes pigmented two days later than controls. When the yolk had been completely utilized, the enlarged sinus shrunk and was no longer seen.

Larvae placed in distilled water immediately after hatching experienced an enormous swelling of the brain area which consequently burst. Thus immediately

after hatching the larvae cannot withstand extreme osmotic stress while older larvae can regulate water flow with greater efficiency. Larvae, regardless of age, have osmolar concentrations in 50% sea water (S = 17‰) equal to that in sea water.

(c) Oxygen consumption in diluted and normal sea water

Theoretically, diluting sea water until it is isotonic with sardine eggs and larvae should result in their consuming less oxygen (NICOL, 1960). Our results (Table 4) show no consistent difference between eggs of the same stage tested in two salinities. Larvae and Stage IV embryos actually seemed to have a

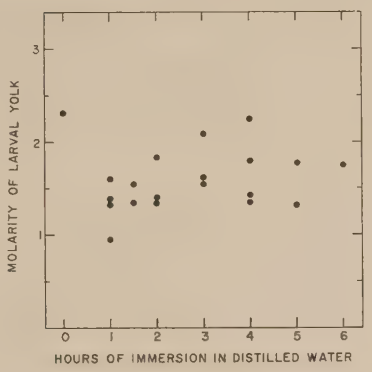

Figure 5. Osmolar concentrations of sardine larvae in distilled water. The dot at "zero hours" is the mean osmolar concentration of 28 control animals with a standard deviation of ± 0·04 M. All other dots represent single animals.

Table 4

Q_{O_2} in µl O_2/mg dry wt/hr of quiescent eggs and larvae in sea water (S = 35‰) and 50% sea water. Each value represents a different individual

	Developmental stage		
	IV	VII	Post hatch larvae
Age in hours	20	37	
Sea water	0·49	0·90	0·82
		1·14	
50% sea water	0·59	0·83	1·00
			1·31
			1·53

Table 5

Respiratory rates of *Sardinops caerulea* eggs at 13·8°C. Warburg manometry; 3 ml of water; shaken at 100 cycles/min; KOH in centre well. Eggs were 45 to 70 hours old (Stage VIII–XI)

No.	Number of eggs	Respiration rates µl O_2/mg dry wt/hr	Conditions
1	103	1·65	sea water
2	132	2·03	sea water
3	22	1·77	sea water
4	102	1·80	half sea water
5	106	1·90	half sea water
6	138	1·80	2 × sea water
7	174	1·90	2 × sea water

slightly higher oxygen requirement in 50% sea water, but the observed differences are not greater than differences usually found between individuals. It was unfortunate that more organisms at the necessary stage and salinity for these experiments did not remain quiescent.

The oxygen uptake of grouped eggs, previously acclimated to isotonic and hypertonic sea waters overnight, was measured with Warburg manometry.

The conditions of the experiment and the results are shown in Table 5. No major differences in oxygen consumption between salinities were noted. The Q_{O_2}'s determined manometrically were similar to those for active eggs measured with the reference diver. All eggs hatched and developed normally after removal from Warburg flasks.

Discussion

FRY (1947) has emphasized the necessity of recognizing the difference between active and standard (resting) metabolism. Although adult fishes have been studied, individual planktonic fish embryos and larvae have not been investigated for active and resting metabolism. In this study we have shown that the active metabolism of sardine larvae may be as much as 3·5 times their resting metabolism. Our data also indicate that there is a considerable variation in oxygen utilization from individual to individual because of spontaneous swimming activity. In laboratory jars larvae whose eyes have not yet pigmented remain suspended motionless for considerable periods. Swimming activity increases as the yolk-sac is consumed and the eyes pigment. BISHAI (1960) has shown that herring, salmon, and trout larvae orient and actually swim into a current. If this is true of sardine larvae they may be constantly swimming and maintaining an active metabolism in nature, unlike their behaviour in laboratory jars.

No conclusive correlation was found between oxygen consumption of larvae in isotonic and hypertonic sea water. From the evidence available we tentatively conclude that the energy requirement for osmoregulation is insignificant when compared to the entire oxygen requirement of the larva.

The embryo and larva of the Pacific sardine, like other clupeids, lack gills, functional kidneys, and a mouth during most of the yolk-sac period. Most pelagic fish larvae seem to be poorly equipped for osmoregulation because of these morphological deficiencies, but it has been suggested that specific cells in the covering epithelium may perform this function until development of regulatory organs (SHELBOURNE, 1957a). SHELBOURNE (1957b) also suggested that the failure of the osmoregulatory process is probably a major cause of heavy mortality among pelagic fish larvae. However, HOLLIDAY and BLAXTER (1960) discount osmoregulatory failure as a prime cause of herring larval mortality, having shown that herring larvae can tolerate wide variations in salinity. Our results with the sardine in general confirm the work of HOLLIDAY and BLAXTER. However, water regulation in very early sardine larvae and eggs is not as good as in older larvae and this suggests that even after hatching they have not developed their full capacity for osmoregulation.

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We are indebted to Mr. Andrew M. VROOMAN and Miss Patricia STRACK for technical assistance, and to Dr. J. S. BRADSHAW for his generous loan of equipment.

Summary

1. The oxygen consumption of 42 single Pacific sardine (*Sardinops caerulea*) eggs and larvae was measured at 14°C with a reference diver technique in

relation to the physiological parameters of swimming activity, age, and osmoregulation.

2. There is a continual increase in oxygen consumption with development and aging of embryos and larvae. Blastodisc eggs consume about 0·5µl/mg dry wt/hr increasing to 1·7µl/ mg dry wt/hr for quiescent larvae 190 hours old.

3. Swimming activity by larvae results in increased oxygen consumption up to 3·5 times that of quiescent larvae.

4. Although sardine embryos and larvae have none of the adult organs for osmoregulation, they maintain a hypotonic internal concentration averaging 0·24 M in 0·56 M sea water. The chorion is freely permeable to water and salts.

5. Eggs stripped of their chorions and early post-hatched larvae swell and burst in distilled water while older larvae do not swell and appear to regulate water flow efficiently.

6. Diluting sea water to isotonicity with eggs and larvae has no marked effect on oxygen consumption.

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The fatty acid composition of the lipids of some Pacific sardine tissues in relation to ovarian maturation and diet

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SUMMARY

Gas-liquid chromatographic analyses of the C_{12} to C_{22} saturated and unsaturated fatty acids of lipids from Pacific sardine ovaries, mesenteric fat, whole blood, and planktonic eggs are presented and compared. Lipids from planktonic eggs and ovaries, with ova in different stages of maturation, have strikingly similar and constant fatty acid compositions. Changes are shown to occur in the fatty acid pattern of mesenteric fat, blood, and ovarian lipids when sardines are fed an artificial diet rich in oleic and linoleic acids. Lipids from sardines fed chiefly on a natural crustacean diet were analyzed for comparison. In general, whole blood lipids have a fatty acid composition similar to the ovary; mesenteric fat differs from ovarian and blood lipids by having a lower content of linoleic acid.

In the Pacific sardine, *Sardinops caerulea* Girard, the gonads increase greatly in weight and size preparatory to spawning. Each ripening egg contains a small (0.2 mm diameter) oil droplet. After the eggs are spawned into sea water and during embryological development, the larvae consume the oil and the proteinaceous yolk. An active synthesis and turnover of organic constituents seem likely during ovarian deposition of this oil. Although the complex mixture of fatty acids in fish fats seems to reflect the composition of the fat in the food eaten (1), fishes occasionally alter the fatty acid composition of their fat by virtue of their own metabolism (2).

The purpose of this study was to investigate the changes occurring in the fatty acid composition of lipid during its deposition in the maturing sardine ovary. Because diet usually alters the fatty acid composition of fish lipids, an artificial diet was fed to sardines and its effect on mesenteric fat, blood, and ovarian lipids was examined.

EXPERIMENTAL PROCEDURE

Saponification and Methylation. Approximately 0.6 g of sardine ovary was added to a 15-ml centrifuge tube containing 5 ml 2.5 N KOH in 85% methanol. The tube contents were occasionally stirred and kept at 75° in a waterbath. After cooling, the nonsaponifiable materials were extracted with three successive washes of 2 ml petroleum ether. Washes were conveniently removed with long-needled hypodermic syringes. The sample was acidified with 3 ml 5 N H_2SO_4. The fatty acids were removed with three 2-ml washes of petroleum ether. After the combined petroleum ether extracts were evaporated almost to dryness, 2 ml of 1% H_2SO_4 in methanol was added and the mixture kept at 75° for 1 hour to complete methylation. The volume was then reduced to about one-fifth of the original, water was added, and the methyl esters were extracted with three 2-ml rinses of petroleum ether. In all operations, mild centrifugation was used to effect sharp interfaces between immiscible solvents. The entire experimental procedure was performed under nitrogen.

Hydrogenation. Complete hydrogenation of the unsaturated fatty acids of sardine mesenteric fat was accomplished by the method of Farquhar *et al.* (3) in a Warburg manometer as suggested by Mead and Howton (4). This method utilizes the Warburg manometer for visualizing the hydrogenation reaction and its completion. Positive identification of chain length for each saturated and unsaturated fatty acid was

possible by gas-liquid chromatography (GLC) after hydrogenation.

Extractions. We found that extraction of sardine tissues with fat solvents such as chloroform-methanol, 2:1 (v/v), petroleum ether, or diethyl ether, was time-consuming and incomplete, particularly when complete homogenization of tissue was not possible. The extractions effected by these methods, however, although incomplete, showed upon analysis the same relative proportions of fatty acids as did the KOH digestion procedure described above.

Gas-Liquid Chromatography. An Aerograph® gas-liquid chromatograph[1] was used to separate and identify the fatty acids. Two columns were used, with helium as the mobile phase: a butanediol-succinate column, which gave excellent separation of the longer chain unsaturated methyl esters, and a silicone-Dow 11 column, which gave precise chain-length information. Columns consisted of 20% stationary phase coated on 60 to 80 mesh firebrick and were 5 feet in length. Helium flow was 35 ml per minute at 204°. Samples were dissolved in 2 to 10 μl hexane for injection.

The logarithmic retention times of sardine fatty acid methyl esters were compared with those of known mixtures run on the same column under the same conditions prior to analysis of a sample. Chain length was confirmed with GLC by a plot of the logarithmic retention time of a completely hydrogenated sample. In all cases, retention times matched those of purified fatty acid methyl ester standards: laurate (12:0), myristate (14:0), palmitate (16:0), stearate (18:0), arachidonate (20:4), eicosapentaenoate (20:5), and docosahexaenoate (22:6).[2] A chromatogram of sardine planktonic egg fatty acids is shown in Figure 1. Quantitative estimates of individual fatty acids were obtained by the triangulation method described by Farquhar *et al.* (3).

Ovarian Development. The stage of ovarian development was determined for each ovary by microscopic examination and measurement of the ova. The yolk diameter of the largest eggs was recorded. Thus, a series of ovaries having eggs with yolk diameters ranging from 0.5 mm in diameter to 1.04 mm in diameter was obtained and analyzed for fatty acids. The ova of one ovary appeared to be in the process of degeneration or resorption. The eggs were smaller than 0.4 mm in diameter; some contained yolk, but the yolk was without the smooth granular appearance common to developing ova.

[1] Wilkins Corp., Walnut Creek, California.

[2] Obtained from the Hormel Institute, University of Minnesota, Austin, Minnesota.

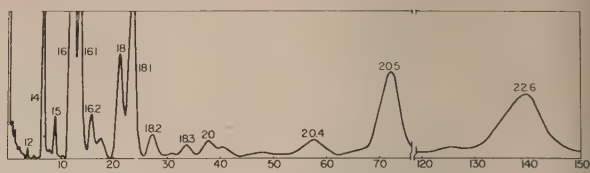

FIG. 1. Gas-liquid chromatogram of saturated and unsaturated methyl esters obtained from sardine planktonic eggs. Ten-minute intervals are indicated on the abscissa. Five-foot column of 20% butanediol-succinate, coated on 60 to 80 mesh firebrick; helium flow, 35 ml per minute; temperature, 204°.

RESULTS

Fatty Acids of the Sardine Ovary and Fertilized Eggs. Sardine ovaries in any stage of maturation, and even in a possible state of resorption, present strikingly similar fatty acid patterns (Table 1). The one ovary identified as "resorbing" showed no significant difference in any fatty acid constituent from any other ovary tested.

It was important to ascertain whether the oil in the individual eggs was similar to, or different from, that found by examining whole ovaries. Newly spawned and fertilized eggs were separated manually from plankton hauls and analyzed for fatty acids. The results are also shown in Table 1. The oil in planktonic sardine eggs is very similar in all components to ovarian lipid in any stage of ova development.

Effect of Diet. Lovern (5) presented convincing evidence that the fat of ingested copepods is deposited largely unchanged by herring. Hand and Berner (6) found that the diet of the adult Pacific sardine is comprised largely (over 80%) of small copepods. A comparison of the fat of *Calanus helgolandicus*, taken in a net haul off San Diego, with the average fatty acid composition of lipids found in sardine ovaries (Tables 1 and 2), shows that there is a great similarity in percentage composition between most of the fatty acid constituents, although some differences exist in the myristic and stearic components. *Calanus* fat serves as an illustration of the kind of fat ingested by sardines in nature. The close correspondence of the fatty acid constituents of the sardine ovarian lipid to those of *Calanus* is good evidence that deposition of dietary fat probably proceeds in the sardine, as in the herring, without major alteration; nor does the fat become altered significantly by the special production of oil for the eggs. Blood taken from a San Diego Bay sardine and from one caught off Santa Barbara, California (Table 3), showed much the same fatty acid composition as did the gonads. This suggests that mobilization of fats from the intestines to the ovaries is relatively direct.

TABLE 1. Percentage Fatty Acid Composition of Sardine Ovaries and Planktonic Eggs*

Whole Ovaries	14:0	†	15:0	†	16:0	16:1	16:2	†	18:0	18:1	18:2	18:3	18:4‡	20:0	20:4	20:5	21:0‡	22:5	22:6
1. 0.5 mm§	4.6	0.0	0.6	0.0	33.0	7.2	1.4	1.0	5.0	9.6	1.5	0.7	0.3	1.2	1.2	15.4	0.0	0.0	17.4
2. 0.7 mm	5.3	0.3	0.9	0.1	39.6	9.1	1.8	0.9	4.7	9.4	1.1	0.6	0.4	0.9	1.3	9.6	0.0	1.6	12.3
3. 0.7 mm	4.8	0.2	0.8	0.2	39.0	8.9	2.0	1.0	4.8	11.2	0.8	0.4	0.3	0.5	1.5	10.2	0.0	2.4	11.0
4 0.8 mm	4.1	0.2	0.9	0.2	40.6	8.8	2.1	1.3	4.8	10.2	0.9	0.2	0.5	0.8	1.3	9.8	0.0	0.5	12.7
5. 1.04 mm	3.6	0.3	0.7	0.1	37.6	7.1	1.5	0.6	4.9	10.4	0.8	0.5	0.4	1.2	1.0	13.4	0.0	1.2	14.8
6. 1.04 mm	4.8	0.2	0.7	0.1	38.5	7.0	1.7	0.6	5.1	9.9	1.3	0.5	0.4	1.6	1.5	13.0	0.0	1.6	11.6
7. Planktonic sardine eggs	3.8	0.3	0.8	0.1	36.4	6.7	1.7	0.9	5.0	9.5	1.3	0.7	0.4	1.2	2.2	12.7	0.2	1.2	15.0
8. "Resorbing" ovary	3.9	0.3	0.9	0.4	32.8	8.4	2.2	1.0	5.5	9.6	0.9	0.4	0.2	0.7	1.9	13.6	0.0	0.0	17.2
Average (ovaries & eggs)	4.4	0.2	0.8	0.2	37.2	7.9	1.8	0.9	5.0	10.0	1.1	0.5	0.4	1.0	1.5	12.2	0.1	1.1	14.0

* Acids present in concentrations of 0.1% or less have been omitted.
† Denotes unidentified fatty acid.
‡ Tentative identification.
§ Diameter of largest yolk.

A test of the effect of diet on the composition of ovarian fat, mesenteric fat, and blood fat of the sardine was made. Depot fatty acids are known to vary with diet in some fish (7, 8, 9). Adult sardines were fed trout food[3] exclusively for three months. Sea water, however, was pumped directly into the sardine holding tank, and it is possible that planktonic food was present. The amount of trout food fed daily was enough to cram the stomachs of the fish, and it is concluded that most, if not all, of the food of these fishes was trout food.

Trout food is very rich in oleic (18:1) and linoleic (18:2) acids but poor in stearic (18:0) and the unsaturated eicosapentaenoic (20:5) and docosahexaenoic (22:6) acids. The complete analysis is given in Table 2.

In trout food, 18:2 is in much greater relative quantity than in any sardine tissue tested. The mesenteric fat laid down by sardines fed on trout food contained at least 3 times the quantity of 18:2 usually found in sardines feeding in the sea. Marked reductions in 20:5 and 22:6 occurred in the ovaries, mesenteric fat, and blood, and are correlated with the low quantity of these substances found in the food. These results are summarized in Table 4.

One consistent difference between mesenteric fat and ovarian fat is that the former contains a high quantity of 18:1 regardless of diet, while the latter seems to respond to the diet (Table 4).

The high resolving power of GLC permitted the identification of most of the saturated and unsaturated fatty acids of the sardine. The occurrence of odd-numbered carbon fatty acids has been demonstrated in menhaden (10, 11) but not previously in sardine tissues. Pentadecanoic acid (15:0) appeared in small quantities in every sardine tissue we tested. Heneicosanoic (21:0) was tentatively identified in planktonic eggs, mesenteric fat, and blood.

A number of fatty acid constituents appeared in small quantities and are as yet unidentified. Three peaks appeared in trace amounts on the chromatograms after 12:0 and are probably C_{12} unsaturated fatty acids judging from their positions and disappearance after hydrogenation. A peak after 14:0 was also probably unsaturated. One C_{18} unsaturated compound, making up less than 1% of the total fatty acids, was tentatively identified as 18:4. The substances appearing after 15:0 and 16:2 could not be hydrogenated.

Stoffel and Ahrens (11) reported 16:3 and 16:4 in menhaden body oil as 1.3% and 2.0%, respectively, of the total fatty acids. We could not separate these acids from the others in sardine lipids, because they are probably masked by the stearate and oleate peaks. Where stearate is low (e.g., in *Calanus* lipid, Table 2) a significant error may be introduced in the reported quantity of stearate. Our conclusions, however, remain unaffected by this possible source of error.

DISCUSSION

Brocklesby and Harding (12) published an analysis of oil obtained as a commercial product from Pacific sardines. Our results differ in certain important respects from theirs. They found a considerable amount (15.2%) of C_{24} unsaturated acid in British Columbia sardines. We have never observed this

[3] Rangens' complete fingerling food.® Rangens' Inc., Buhl, Idaho.

TABLE 2. PERCENTAGE FATTY ACID COMPOSITION OF THE COPEPOD *Calanus helgolandicus* AND TROUT FOOD*

	12:0	14:0	†	15:0	†	16:0	16:1	16:2	†	18:0	18:1	18:2	18:3	18:4‡	20:0	20:4	20:5	21:0‡	22:5	22:6
Calanus helgolandicus	0.2	10.7	0.9	0.8	0.2	34.6	8.2	0.5	0.2	1.6	7.3	1.1	0.5	1.3	1.7	0.3	14.3	0.2	0.0	15.4
Trout food	0.2	4.3	0.2	0.3	0.1	27.1	3.4	1.0	0.8	2.9	25.2	26.1	1.8	0.0	2.2	0.0	2.0	0.0	0.0	0.8

* Acids present in concentrations of 0.1% or less have been omitted.
† Denotes unidentified fatty acid.
‡ Tentative identification.

TABLE 3. PERCENTAGE FATTY ACID COMPOSITION OF SARDINE MESENTERIC FAT AND WHOLE BLOOD*

Fish No.	Tissue Analyzed	12:0	14:0	†	15:0	†	16:0	16:1	16:2	†	18:0	18:1	18:2	18:3	18:4‡	20:0	20:4	20:5	21:0‡	22:5	22:6
1.	Fat ♀	0.1	6.1	0.4	0.6	0.1	28.0	4.9	2.3	1.3	5.4	20.3	2.3	2.0	2.1	3.8	0.1	10.9	1.2	1.4	6.9
2.	Fat ♂	1.0	3.4	0.5	0.6	0.1	27.3	10.9	1.4	0.6	3.5	32.1	0.5	0.3	0.3	1.0	0.2	8.5	0.0	0.6	7.4
3.	Fat ♀	0.1	6.6	0.1	0.4	0.0	32.2	5.0	2.3	1.2	8.1	18.4	1.0	0.7	2.8	1.7	0.2	10.3	0.7	2.2	6.2
4.	Whole Blood ♀§	0.1	3.8	0.1	0.4	0.1	36.7	5.0	1.6	0.6	5.0	8.8	0.4	0.4	0.3	1.8	0.9	13.2	0.6	1.1	19.5
5.	Whole Blood‖	0.4	4.9	0.1	0.5	0.1	30.7	5.6	2.3	0.1	4.6	6.7	0.6	0.1	0.5	1.6	1.5	20.2	0.0	0.0	19.6

* Acids present in concentrations of 0.1% or less have been omitted.
† Denotes unidentified fatty acid.
‡ Tentative identification.
§ San Diego fish.
‖ Sex unknown, Santa Barbara fish.

fatty acid in our sardines. Their report of 14.4% of palmitic acid should be contrasted with our analyses showing an average quantity of 37% for sardine ovaries. However, Hart and Wailes (13) have shown that sardines taken in British Columbia feed chiefly on diatoms during the summer. This may have influenced the fatty acid composition of the fish.

Our sardines were selected at random from those collected by bait boats in the San Diego area. In any single school a large variation can exist in the degree of gonad maturation and in the amount of mesenteric fat present. The ovaries analyzed were selected according to maximum egg size to provide a complete range of maturation. No systematic difference in any fatty acid was discovered as ovary maturation proceeds; all the ovaries tested had remarkably consistent fatty acid patterns. This consistency may be the result of a similarity in diet in all these fishes and serves to emphasize the small metabolic control exerted over fatty acid deposition in the ovary.

The difference found in 18:1 in the mesenteric fat when compared to ovarian fat could be the result of a metabolic emphasis on storage of fatty acids in C_{18} form. If so, this may mean that mesenteric fat does not contribute to the fat of the ovary directly but is used chiefly for energy by the fish. Lovern (14, 15) found that changes appear in salmon-egg oil as the eggs develop and that, as ripening proceeds, there is a marked rise in the proportion of C_{18} acids, while, at the same time, unsaturation decreases. This change is in marked contrast to the present findings.

TABLE 4. PERCENTAGE COMPOSITION OF FOUR FATTY ACIDS IN INDIVIDUAL SARDINES AS RELATED TO DIET

Tissue	Conditions	18:1	18:2	20:5	22:6
Mesenteric fat ♀	Crustacean-fed	20.3	2.3	10.9	6.9
Mesenteric fat ♂	Crustacean-fed	32.1	0.5	8.5	7.4
Mesenteric fat ♀	Crustacean-fed	18.4	1.0	10.3	6.2
Mesenteric fat ♀	Trout food-fed	32.8	11.1	1.5	0.8
Mesenteric fat ♀	Trout food-fed	22.6	8.1	7.3	1.4
Ovary*	Crustacean-fed	10.0	1.1	12.2	14.0
Ovary	Trout food-fed	20.3	3.7	7.2	11.4
Ovary	Trout food-fed	21.1	7.1	8.6	6.4
Blood ♀	Crustacean-fed	8.8	0.4	13.2	19.5
Blood ♀	Trout food-fed	13.7	4.2	4.1	1.8
Calanus		7.3	1.1	14.3	15.4
Trout food		25.2	26.1	2.0	0.8

* Average of all ovaries listed in Table 1.

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Sexual Maturity as Determined from Ovum Diameters in Striped Bass from North Carolina

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ABSTRACT

Sexual maturity of striped bass, *Roccus saxatilis* (Walbaum), was investigated in the Albemarle Sound–Roanoke River system of North Carolina during the periods October 1956 through January 1957, October 1957 through April 1958, and April through September 1960. A method which permitted the determination of maturity through the measurement of ova was used. Percentages of mature female fish during several months prior to spawning are given by age group. At age-group VII and older, there was evidence of intermittent spawning and the possibility of cessation.

INTRODUCTION

Important sport and commercial fisheries for striped bass, *Roccus saxatilis* (Walbaum), exist in the Albemarle Sound–Roanoke River system of North Carolina. Studies of population dynamics are being conducted by the U. S. Bureau of Commercial Fisheries to evaluate the effects of fishing upon the exploitable fish in the population. As part of the research program a study was made to determine the number of years striped bass are exploited by the commercial fishery in Albemarle Sound before first spawning in the Roanoke River (April, May, and June), and to develop criteria for sexual maturity.

Scofield (1931) presented selected data which showed the probable development rate of striped bass ova. Jackson and Tiller (1952), in a preliminary study of female striped bass, predicted that ova containing yolk material and averaging 0.180 to 0.190 millimeter in diameter would take approximately 1 year to develop.

Samples from ovaries were examined in the present study to determine how effectively the size and appearance of striped bass ova in the Albemarle Sound–Roanoke River system could be used as criteria of sexual maturity, and to estimate the proportion of sexually mature female striped bass in each age group.

MATERIALS AND METHODS

Samples of ova were obtained from commercial catches of striped bass during the period October 1956 through January 1957, October 1957 through April 1958, and April through September 1960.

The size of fish available for sampling varied because of a change in gill-net size fished. Most fish caught during the fall and winter by the commercial fishery are taken with gill nets having mesh sizes from 3¾ to 4¼ inches (stretched measure). In the spring, with the beginning of fishing for American shad (*Alosa sapidissima*), the commercial fishery also uses gill nets with mesh sizes up to 5½ inches (Sykes and Davis[1]). As a result, larger striped bass are caught in the spring than in the fall.

Fragments of gonads were extracted from the coelom with ear forceps inserted into the vent and through the intestinal wall. Sex was determined by microscopic examination of preserved gonadal fragments according to the method described by Sykes (1958). Both male and female gonads were examined, but only females could be used in the determination of sexual maturity.

At least 100 ova were selected randomly from each ovarian sample, and were measured on a grid-etched slide with a 45× dissecting microscope containing an ocular micrometer. Many of the ova were asymmetrical, so measurements were made parallel to the long axis of the etched slide. This method was similar to that employed by Scofield (1931) and Otsu and Uchida (1959). Merriman (1941) and Jackson and Tiller (1952) measured striped bass ova under a compound microscope with an ocular mi-

[1] Sykes, James E. and William S. Davis. (1960) Commercial harvest and catch composition of striped bass in Albemarle Sound, North Carolina. U. S. Bureau of Commercial Fisheries, Beaufort, North Carolina. Typewritten report, 44 pp.

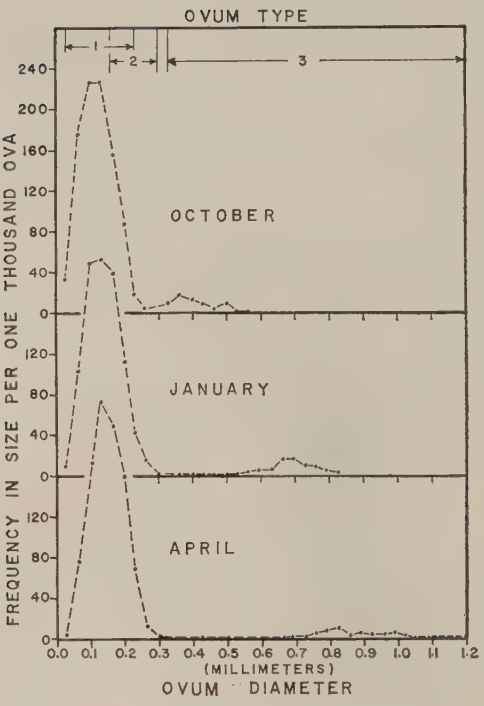

FIGURE 1.—Frequency distribution of ovum diameters from composite samples of striped bass during October, January, and April.

crometer, but did not elaborate on the methods employed.

Scales were obtained from each fish for age determination. Fish were aged according to the number of annuli present and the number of completed growing seasons at the time of capture (Mansueti, 1961). For example, those fish that had three scale annuli but had completed four growing seasons were in age-group IV.

RESULTS

Size and appearance of ova

The following types of ova were identified: (1) translucent ova that ranged in size from 0.03 to 0.23 millimeter, with a mode at approximately 0.10 millimeter; (2) translucent ova that ranged between 0.16 and 0.30 millimeter and in which the yolk had begun to form as opaque speckling; and (3) opaque ova that ranged from 0.33 millimeter to approximately 1 millimeter. No ova were found between 0.30 and 0.33 millimeter.

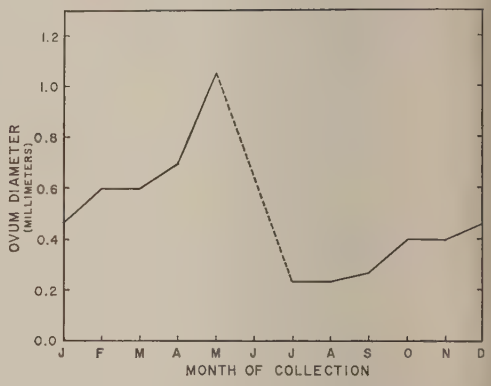

FIGURE 2.—Minimum size of largest type 2 or type 3 ova from monthly samples of mature female striped bass in Albemarle Sound. No samples were available in June (dashed line).

The diameter frequency from composite samples was plotted to show sizes of ova encountered in three months prior to spawning (Figure 1). It was found that each fish had only one of the following categories of ovaries: (1) those that contained only type 1 ova; (2) those that contained types 1 and 2; and (3) those that contained types 1, 2, and 3. Type 1 ova were found in all ages and sizes of striped bass. Type 2 ova were found during all months of sampling. Some type 2 ova developed into type 3 ova during the 3 months immediately after spawning. The remainder continued in type 2 throughout the year. A steady increase was found in the maximum size of the largest type 3 ova as the spawning season approached. Most fish were above 17 inches fork length, and were at least in age-group III before ovaries with type 3 ova were found.

The minimum size of the largest ova present in Albemarle Sound fish was determined by sampling each month throughout the year except during June when no samples were available (Figure 2). Ovum growth began slowly in the summer and fall, but increased rapidly as the spawning season approached. Apparent inflections in the curve are probably due to sampling error.

Type 3 ova collected from fish taken in the Roanoke River during the spring were between 0.80 and 1.50 millimeters in diameter at the time of spawning, and they averaged approximately 1 millimeter. Growth of the

TABLE 1.—*Numbers of immature (I) and mature (M) female striped bass collected in Albemarle Sound by month during 1956–57 and 1957–58*

Age-group	1956–57								1957–58													
	October		November		December		January		October		November		December		January		February		March		April	
	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	M
II	13	0	16	0	13	0	7	0	23	0	22	0	25	0	58	0	17	0	38	0	11	0
III	45	0	113	5	20	1	47	2	2	0	46	1	24	0	53	5	5	0	61	2	9	0
IV	1	2	1	5	0	1	2	6	0	0	3	5	1	2	1	6	0	10	4	65	1	64
V	0	1	0	3	0	3	0	0	0	0	0	1	0	0	0	0	0	2	0	27	0	12
VI	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	2	0	8	0	2
VII and older	0	2	0	0	1	2	0	1	0	0	1	1	0	1	0	3	0	1	0	2	0	2
Totals	59	5	130	13	34	8	56	10	25	0	72	9	50	3	112	15	22	15	103	104	21	80

ova from approximately 0.20 to 1 millimeter occurred between spawning seasons (Figure 2). Therefore the following maturity criteria were established: (1) if the largest type 2 or type 3 ovum found was equal to or greater than the minimum size of ova for a given month as shown in Figure 2, it was presumed that the fish would spawn the following spring, and the fish was considered mature; (2) fish with small translucent ova only were considered immature fish which would not spawn for at least a year following the coming spawning season. Thus fish with type 1 ova are immature, and those with types 2 and 3 are mature.

Other workers have also established criteria to indicate spawning potential in striped bass. Their findings support those of the present study. Scofield (1931) found that striped bass with ova exceeding 0.29 millimeter were spawners in California. His conclusions were based in part on a comparison of the percentage of fish in spawning and non-spawning condition before and after the spawning season. Jackson and Tiller (1952) stated that striped bass from Chesapeake Bay having ova averaging 0.75 millimeter or more in diameter in early spring could be expected to spawn that year. In our study, fish with ova averaging 0.70 millimeter and showing external evidence of becoming ripe were found in March and April in Albemarle Sound. These ova would have increased in size to full maturity during the spawning season of that year.

Differences within type 1 ova

The occurrence of two sizes of type 1 ova in striped bass depended upon whether or not the fish were sexually mature. The only ova found in immature fish were those of type 1 which averaged 0.086 millimeter in diameter. Mature fish had type 1 ova which averaged 0.124 millimeter in diameter plus at least one of the other two types. The average difference between type 1 immature and type 1 mature ova was 0.038 millimeter. Scofield (1931) reported that small ova in striped bass collected in California averaged 0.125 millimeter. Merriman (1941) and Jackson and Tiller (1952) reported 0.07 millimeter as being the average size of small ova for striped bass collected in Connecticut and Maryland. None of these researchers reported two size groups of type 1 ova.

Age of spawners

Female striped bass were categorized by age groups as mature and immature fish (Table 1). The percentages of mature fish are presented by age group in Figure 3. Three and four percent of age-group III fish

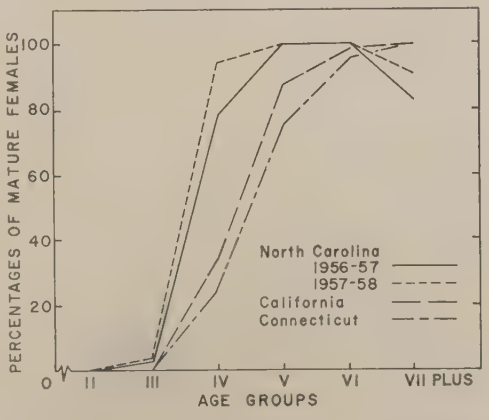

FIGURE 3.—Percentages of mature female striped bass by age from different regions.

were capable of spawning subsequent to the commercial fishing seasons of 1956–57 and 1957–58. Seventy-eight and 94 percent of age-group IV were mature, and all fish of age-groups V and VI were mature. In age-group VII and older, one of the six fish taken in the first year of sampling and one of the eleven fish taken in the second year contained no type 3 ova.

The percentages of spawners found by workers in different regions varied by age group. In our study of North Carolina fish, some of those in age-group III were found to be capable of spawning, but none capable of spawning at that age were found in other regions (Figure 3). Both spawners and non-spawners were found among age-groups IV, V, and VI in Connecticut (Merriman, 1941) and in California (Scofield, 1931). Spawning by all females was indicated first at age-group VII by these workers, and at age-group V in the present study.

A difference also occurred in the percentage of age-group IV spawners from the different regions. A higher percentage of fish from this age group were mature in North Carolina than in the other regions. A similar but smaller difference occurred for the age-group V fish. In age-group VI there were no major differences in the percentage of spawners from various regions. In Maryland, Jackson and Tiller (1952) found that most females spawned by the time they entered age-group IV or V, and that striped bass from this area were consistent spawners in age-groups VI through X, but these workers did not state the percentage of mature fish in individual age groups. Jackson and Tiller also suggested that a reduction in ova production may occur in some individuals after age-group X. The present study in North Carolina also indicates that some of the older fish do not spawn annually.

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ROBERT LIVINGSTONE, Jr.

UNDERWATER TELEVISION OBSERVATIONS OF HADDOCK (*MELANOGRAMMUS AEGLEFINUS* [LINNAEUS]) IN THE COD-END

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Underwater Television Observations of Haddock (*Melanogrammus aeglefinus* [Linnaeus]) in the Cod-End

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Introduction

It has been adequately demonstrated by many investigators (Clark, Mc Cracken, and Templeman, 1958) that fish of many species will, under the proper conditions, escape through the meshes of otter trawl nets. It is not clear, however, to what extent the degree of escapement is dependent upon the behaviour of the particular species. In many fisheries behaviour plays an important role. The meshes of the leads of the pound net, for instance, are sufficiently open to permit fish to pass through them, but most species do not attempt to do so. Herring schools have been successfully herded by a curtain of air bubbles (*World Fishing*, 1960). New Zealand trawl and lampara-net fishermen are reported to have used meshes in the wings as large as 92 to 183 cm with no apparent loss to the catch (Cassie, 1955, p. 16).

In discussing the escapement of fishes through meshes of otter trawls, the problem of fish behaviour was considered by the Joint Scientific Committee[1]) in 1957 at Lisbon, Portugal. The following questions were some of those asked (ICNAF, 1960):

"Do fish try to escape or are they carried passively through the meshes?"

"Do different species have different behaviour patterns which affect the probability of their escape?"

"If many fish enter the net simultaneously, how do they affect each other's efforts to escape?"

"In what directions do fish swim in relation to the net, and is there some critical angle of approach beyond which escape is impossible?"

[1]) Consisting of International Commission for the Northwest Atlantic Fisheries, International Council for the Exploration of the Sea, and Food and Agriculture Organization of the United Nations.

Following the "Lisbon Meetings" personnel of the Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Massachusetts, made a special underwater television cruise ("Albatross III", Cruise XCVI, June 1957), to observe the reactions of groundfish to chafing gear and other cod-end covers. CLARK (1958) reported on the effect of chafing gear on escapement of haddock and LIVINGSTONE (1959) discussed several behaviour patterns inside the cod-end. The present report describes haddock behaviour in the cod-end in relation to escapement and is based on a critical analysis of films taken of the television monitor during one tow.

Material and Methods

The television camera was mounted inside the cod-end (CLARK, LIVINGSTONE, and CROSSEN, 1960), of a No. 41 "Yankee" trawl (Figure 1). The camera, an image orthicon (5820) requiring approximately 5·4 m.c. (0·5 ft. c.) subject illumination for a useable picture, viewed the central passage of the cod-end aft and covered a maximum viewing angle of approximately 45 degrees. The cod-end of 114 mm (knot to knot, stretched internal measurement) dacron mesh extended 6·1 m out from the camera window to the end of the cod-end. It was covered by 38 mm cotton webbing in the manner described by CLARK (1957). Most of the lower side of the cod-end was protected by bull hides.

The trawling experiment was conducted in a small area about 5·6 km east of Cape Cod (41°52′N; 69°53′W) in depths of 31 to 38 m. The trawl was towed on various courses and at various speeds ranging from approximately $1\frac{1}{2}$ to $3\frac{1}{2}$ knots.

The behaviour of fish was recorded in writing and at intervals by motion picture photography of the television image. All observations were made between 8:00 a.m. and 11:00 a.m. using natural illumination only. Films were made with a spring-driven 16 mm camera mounted in front of the television viewing screen and operated at 24 frames per second (CLARK, *et al.*, 1960). One winding operated the camera for about 30 seconds.

In the laboratory the films were first projected with a standard 16 mm projector to determine the subject content and quality. Next, each sequence was arranged and marked at the point on the film where winding breaks (usually a clear frame) occurred. Once the film sequences were so arranged, they were studied in a film editor equipped with a frame counter. The number of frames, when related to the running speed of the film, made it possible to time the activities of the fish.

In particular, the following details of behaviour were noted: –

Rate of entry of fish into the cod-end. This was determined by dividing the total number of fish in a sequence by the total number of frames in that sequence (converted to time at the rate of 24 frames per second).

Position of entry into the cod-end and orientation. The television camera was located at the centre of the cod-end, and fish were recorded as entering either the top or bottom half of the cod-end. The orientation or direction the fish was facing as it entered the cod-end was noted as follows: upstream-fish faced forward; downstream-fish faced aft; cross stream-fish faced sideways.

Swimming patterns and other behaviour. Fish reactions and movement were analysed to determine the typical swimming patterns.

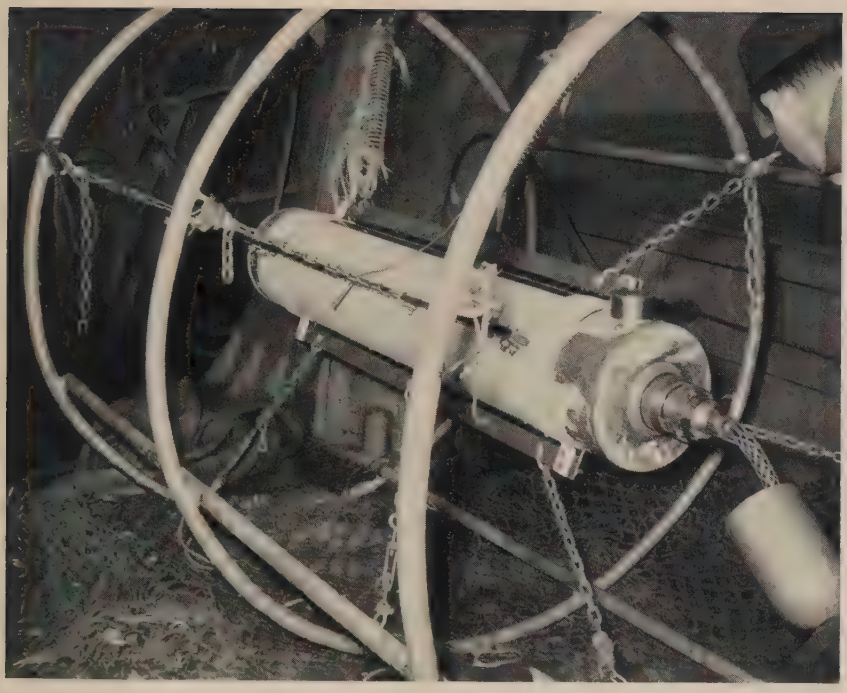

Figure 1. The television camera unit in its frame. The cod-end is lying on the deck.

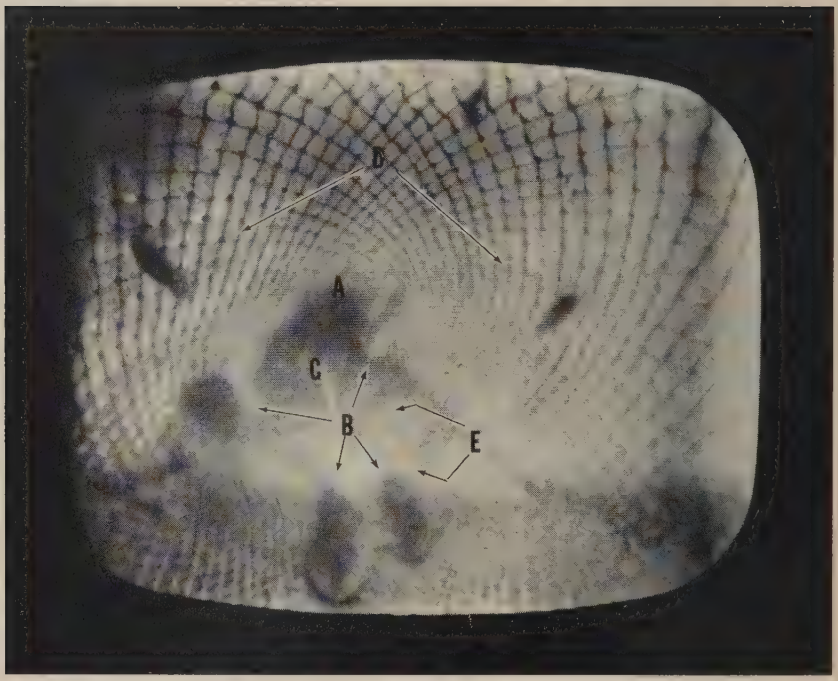

Figure 2. Looking aft inside the covered cod-end. The cod-end extends approximately 6·1 m from the camera; the tunnel (A) is about 3·7 m from the camera and leads into the after portion where the catch accumulates. The fish (B) are haddock facing upstream; (C) a lone sand-eel (*Ammodytes* sp.), and squid (D) hanging at the sides. The flapping at the loose end of the bull hide causes a sand cloud (E).

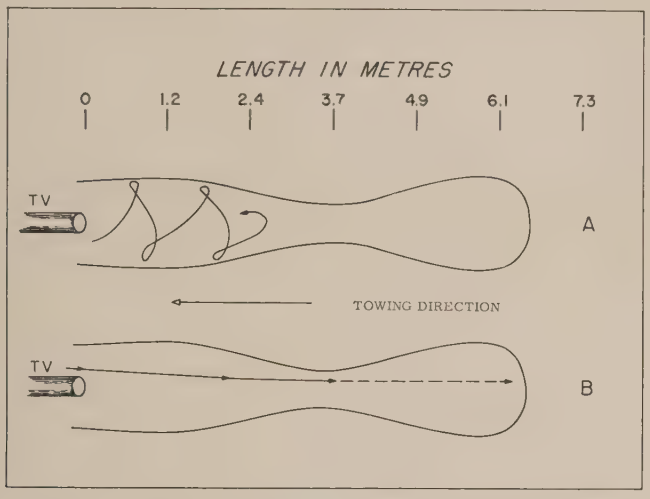

Figure 3. Top view of cod-end and television camera showing; (A) lateral swimming pattern and (B) a downstream pattern (diagrammatic).

Final disposition. The location and orientation of the individual fish at the end of each observation were noted where possible. Some were either lost from view among the mass of individuals in the cod-end, or they moved out of range of the television camera's field of view and were not seen again. In these instances final disposition was recorded as "undetermined."

Also uncertain was the final disposition of haddock that entered the "tunnel" leading into the end of the cod-end. This tunnel becomes apparent as the catch accumulates, the accumulation resulting in the somewhat tapered appearance of the mid-section of the cod-end as shown in Figure 2 and diagrammatically in Figure 3.

Results

Most haddock were in view for relatively short periods, ranging from 0·4 to 28 seconds, with an average time of about 7 seconds.

Grouping of haddock and rate of entry. Haddock entered the cod-end in loose groups numbering between 3 to 26 individuals. These groups were usually composed entirely of haddock, though scattered sand-eels (*Ammodytes* sp.), and several cod (*Gadus morhua*) were noted as entering at about the same time as the haddock. Individuals in the groups of haddock were spaced as closely as 0·6 second apart; approximately one entered the cod-end every 1·6 seconds.

Entry into the cod-end and orientation. Of the 247 haddock observed, 80% entered the cod-end near the top and 20% entered near the bottom. As to orientation, 49% faced upstream, 36% faced downstream, and 15% faced across stream.

Swimming patterns. Most of the haddock, after passing the camera, swam from side to side, seldom up and down. Movement to the sides depended somewhat on initial orientation and was common (84%) for fish that entered the

cod-end across the stream. Some side to side movements also resulted from fish turning to avoid each other. Two swimming patterns were apparent: –

Lateral swimming pattern. Haddock swam from side to side crossing the cod-end in 0·4 to 1·0 second. For certain individuals these movements lasted up to 8 seconds. Some haddock crossed the net as many as 5 times; the average was 0·9 crossings. The movements frequently described a modified figure "8" path (Figure 3), with a gradual displacement toward the tunnel. This lateral swimming pattern was observed for 52% of the haddock that entered facing upstream, for 29% of the haddock that entered facing downstream, and for 84% of the haddock facing across stream.

Downstream pattern. Of the 89 haddock that entered the net headed downstream, 53% continued in this direction into the tunnel. Haddock headed downstream did not usually change their direction, nor did they touch the meshes (Figure 3). They could not, however, be followed beyond the entrance to the tunnel.

Avoiding reactions. Haddock were able to turn quickly and thus avoid swimming into each other or into the meshes. The avoiding reaction with respect to the mesh was particularly noticeable during lateral swimming. Frequently after haddock crossed the cod-end the first time, they avoided contact with the meshes in the side-to-side movements that followed. Of 229 crossings of the cod-end, 76% were made without contact with the meshes; about 24% collided with meshes, usually on the first crossing. Avoiding reactions between individuals were recorded for 60 fish of which 12% resulted from actual collisions.

Final disposition. The orientation and location of individual haddock in the cod-end at the end of each observation was as follows: –

Action	Number	%
Upstream, actively swimming, not in contact with netting	58	24
Upstream, not actively swimming, just above or in contact with bottom netting	85	34
Downstream, swam or drifted directly to tunnel	75	30
Undetermined (could not follow, film sequence ended, etc.)	29	12

Discussion

Several points need to be clarified before we can discuss the results. It has been previously mentioned that sand-eels were taken in the same tow with the haddock. Sand-eels occurred in immense numbers though, in mass, they usually entered the net at a different time than the haddock. Although no active predation was observed in the net, later examination of stomachs showed that haddock had been feeding on sand-eels. No sand-eels, incidentally, were retained by the cod-end or the cover. Most escaped in less than 2·5 seconds.

From the film we counted 247 haddock. However, after hauling we removed 278 haddock (average 50·4 cm) from the cod-end and 70 (average 34·1 cm) from the cod-end cover. These haddock in the cover were small enough by several centimetres to escape from the 114 mm mesh cod-end (CLARK, *et al.*, 1958, p. 94). Since we saw no haddock escape from the 3·7 m of the cod-end in view, the smaller fish apparently escaped at the end of the net where observations could not be made.

The lateral swimming pattern would presumably enhance escapement and is worth some further comment. Haddock in crossing and recrossing the cod-end often approached the meshes at an approximate right angle. BLAXTER, HOLLIDAY, and PARRISH (1958) found that a similar angle of approach to netting by herring was one of the factors that increased their chance of getting through the meshes. The haddock, however, frequently turned before they touched a mesh and practically always in an upstream direction. Turning upstream often resulted in the haddock attempting to "keep pace" to swim in the same direction the net was moving. Some of the haddock kept pace in midstream and were gradually displaced towards the tunnel. Other settled down and lined up along the bottom of the cod-end or along the laceages (see Figure 2) where they might remain for 15 minutes or longer. A few actually made headway and slipped forward out of view. For the haddock that kept pace, and they represented the majority, there were no serious attempts to escape.

This swimming response by fish to a moving background was considered by LYON (1904) to be based on an optical reflex — the fish moved when its background moved and in the same direction. In one of his experiments LYON placed *Fundulus* in a box that had wire mesh at both ends, gravel on the bottom, and sea lettuce along the sides. When he moved the box through "quiet" water, the fish swam in the direction the box moved. This experiment may be equated with the fish in the cod-end, that appear to be visually orienting to the cod-end moving in an apparent current. Just how long a fish will swim in the same direction as the net will probably depend on the number entering the cod-end, their swimming ability, the incident light level, and the towing speed. It seems reasonable to suspect that such a response might delay active escapement and, in some instances, effectively prevent it. Certainly the data discussed here would indicate that haddock also responded to the background and this behaviour did not lead up to any active effort to escape.

Acknowledgement

For reading the manuscript and helping in field experiments I am indebted to Mr. Albert C. JENSEN of the Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Massachusetts.

Summary

1. The behaviour of 247 haddock entering the cod-end of an otter trawl was observed using a television camera and later studied from films made simultaneously of the monitor.

2. In general, haddock entered the cod-end near the top in loose groups numbering between 3 to 26 individuals, rather than continuously, at an average rate of one fish every 1·6 seconds.

3. Two distinct swimming patterns were recorded; one in which individuals swam from side to side and generally avoided the meshes, and another in which individuals headed downstream to the end of the cod-end.

4. Approximately 58% of the haddock responded to the moving cod-end meshes by keeping pace with the net.

5. Our observations indicate that certain behaviour patterns exist in the cod-end and that these behaviour patterns may be typical of other species also. The need for further behavioural studies to assist in interpreting mesh selection results and in explaining the variations in "escapement values" for different species (cf., CLARK, *et al.*, 1958) is obvious.

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ANDELSBOGTRYKKERIET I ODENSE

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GAMETOGENESIS AND SPAWNING OF THE EUROPEAN OYSTER, O. EDULIS, IN WATERS OF MAINE

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GAMETOGENESIS AND SPAWNING OF THE EUROPEAN OYSTER, O. EDULIS, IN WATERS OF MAINE

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In the late '40's a heavy mortality of an epizootic nature occurred among the populations of the soft clam, *Mya arenaria,* along the New England coast. The mortality was especially serious in the waters of Maine where, in many areas, these clams almost completely disappeared. Since *M. arenaria* was virtually the only commercial mollusk of that state, many shore communities were seriously affected economically. Realizing that economy established on a single shellfishery is insecure, we suggested that the local shellfisheries resources be supplemented by the introduction of another mollusk of commercial promise. We had in mind the European oyster, *Ostrea edulis,* which propagates at a somewhat lower temperature than our native oyster, *Crassostrea virginica.*

The European oysters were shipped to Milford from the Oosterschelde, Holland, in the fall of 1949. Large oysters arrived in good condition and, after resting in Milford Harbor, were planted in Boothbay Harbor and three other locations in Maine (Loosanoff, 1951, 1955). In Boothbay Harbor the oysters grew well and showed comparatively low mortality. Gonadal samples, taken from this group at regular intervals, provided the material for the histocytological studies on which the present paper is based. The tissue was preserved in Bouin's fluid, sectioned at 5 μ, and stained with Heidenhain's iron hematoxylin and eosin.

A description of the sexual phases of the European oyster is not the purpose of this article. This matter has been considered in a number of extremely informative publications, starting with Hoek (1883); Spärck (1925); and, especially, Orton (1927, 1933). Later it was reviewed by Coe (1936). Obviously, it is not necessary to go into the details of this complex problem again. Therefore, this article describes only two important aspects of the behavior of European oysters—gametogenesis and spawning under the new set of ecological conditions encountered in Boothbay Harbor.

It may be appropriate to mention here, chiefly as a reminder, Orton's discovery that the European oyster is protandric, with the sexual phases alternating regularly, in most individuals, after the initial male phase. Under favorable conditions each adult oyster completes one male and one female phase each year. Some oysters function as males early in the spawning season and later change to the female state. Others have the opposite sequence of phases. Because of this situation, individuals of both sexual types are found in the population during the entire spawning season (Cole, 1941).

Orton (1927) also suggested dividing the oysters into approximately eight arbitrary categories based upon the relative numbers of cells of different sexes in their gonads. These categories, which were established principally on studies

of gonadal smears, do not, however, appear to be precise enough if compared to results of similar studies in which regular histological preparations are used. The latter, based on a large number of sections, would show that different portions of a gonad of the same individual may often give an entirely different characterization of the sexual conditions of that individual. In other words, while some portions of the gonadal tissue of an individual may characterize it, according to Orton's standards, as a pure male, another and often closely adjacent portion of the gonad may display purely female conditions. Sometimes, in the same individual the adjacent follicles might contain cells of opposite sexes although the individual, as a whole, is, obviously, ambisexual.

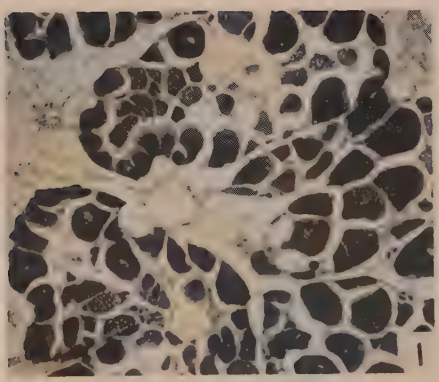
Since virtually all of the Boothbay Harbor oysters studied were ambisexual to some extent, we hesitate to accept the classification of Orton, who assumed that there are pure male and pure female individuals which, presumably, contain exclusively male or female cells, respectively. Accordingly, in this study we shall designate all individuals as representing three chief categories, namely, (a) strongly ambisexual (Fig. 1); (b) predominantly male (Fig. 2); and (c) predominantly female (Fig. 3).

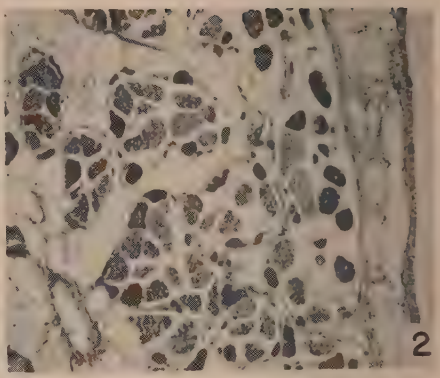
It is convenient for several reasons to begin the discussion of the seasonal sexual changes of the European oysters kept in Boothbay Harbor with the spring gametogenesis. Although in some instances it may begin in April, the population in general does not display early stages of gametogenesis until the latter part of May. Even at that time, approximately 10% of the oysters still possess typical winter follicles, which are small, contracted and surrounded by large masses of connective tissue (Fig. 4). At this time they contain only indifferent cells or gonia, although phagocytic cells are often present in the lumina.

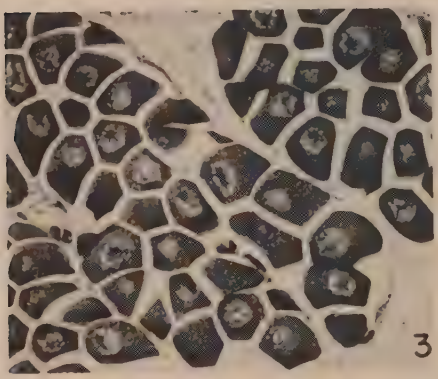
In oysters already undergoing spring gametogenesis, follicles in the same individuals are often in widely different stages of development. Although, in general, they are still small and surrounded by connective tissue, which occupies most of the space between digestive gland and outside membrane of the oyster body, a few sperm-balls are already present in males. In the majority of cases, however, only spermatids or spermatocytes have been formed so far. At this period, developing eggs are usually small, measuring under 50 μ (Fig. 5).

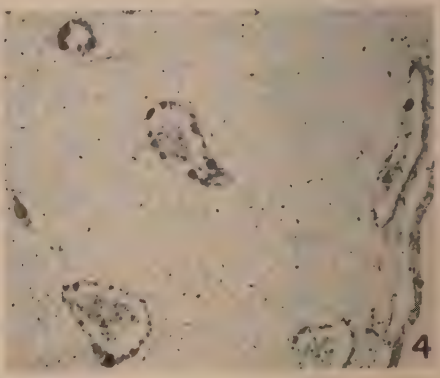
Two basic differences can be noticed between the general structure of the gonads of American and European oysters at this time and, also, later in the season. One is that the tissue layer for potential development of gonad material is significantly thicker in American than in European oysters of the same size. In the latter, the layer of gonadal tissue, *i.e.*, the area demarcated from the outside by the body wall and from the inside by the digestive gland, may very often consist of a single layer of follicles. Actual measurements show that while in American oysters 3″ to 4″ in size the thickness of gonadal layer may often be 3.5 to 4 mm., in European oysters of the same size it rarely exceeds 1.25 mm. Another basic difference is that while in American oysters the follicles are surrounded by a large number of leucocytes (lymphocytes) which probably act as carriers of nutritive material to the developing follicles (Loosanoff, 1942), cells of this type are entirely absent in *O. edulis* (Fig. 6).

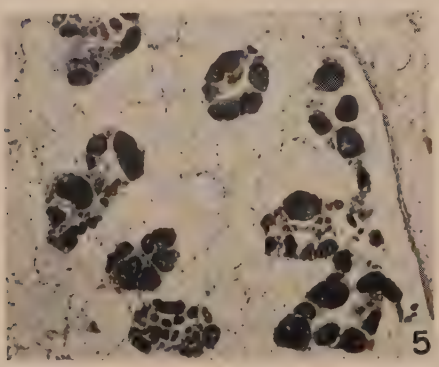
By the middle of June the gonadal layer is still comparatively thin and only in exceptional cases do proliferating follicles extend all the way to the digestive gland.











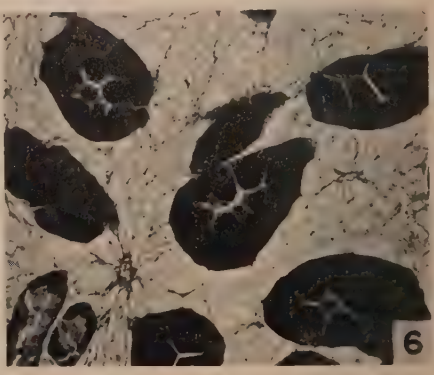


FIGURE 1. Ripe ambisexual gonad of *O. edulis*. Sperm-balls and groups of cells in earlier stages of spermatogenesis are in the center of the follicles. Note connections between blood vessels and apices of the follicles. × 80.

FIGURE 2. Ripe predominantly male gonad of *O. edulis*. Many sperm-balls can be seen in genital canal. × 80.

FIGURE 3. Ripe predominantly female gonad of *O. edulis*. × 80.

FIGURE 4. Winter follicles of *O. edulis* confined between body wall and digestive gland

Nevertheless, more than half of the follicles with male cells contain what appear to be fully developed sperm-balls (Fig. 7). Spermatids become more numerous while primary and secondary spermatocytes begin to decrease in numbers. Eggs measuring between 75 and 100 μ are already found in some individuals, but there is no evidence of spawning.

At the end of June and during the first week of July sperm-balls can be found in the genital canals of some oysters, yet no mass spawning has occurred.

Spawning begins during the second or third week of July and continues until about the end of August (Fig. 8). However, during the first part of this period many oysters are still unripe and gonadal follicles occupy only about half the available space. In many males, even those which have discharged some sperm-balls, large groups of spermatids, and even spermatocytes, are still present.

Toward the end of July unripe oysters are still common but in the group representing only 5 to 10% of the population, spawning is already completed and resorption of gonads is beginning. In the latter individuals shrinking of follicles is in progress and invasion of connective tissue is rapidly taking place. Most of the individuals that have completed spawning are males but, strangely enough, regardless of early completion of the male phase, there is no cytological indication that a female phase will follow. It is probable, therefore, that in many instances, because of our short, cold summers these oysters can complete only one reproductive phase each season.

By the middle of August approximately 75% of the oysters are either partially (Fig. 9) or completely spawned. The majority of the completely spawned individuals, however, are predominantly males. As observed earlier in the summer, it is apparent that the male phase would not be followed by the completed female phase. Only in exceptional cases are small ovogonia or ovocytes seen developing along the walls of the follicles but, due to the lateness of the season, their development cannot progress very far before the onset of winter and relative inactivity.

After completion of the major spawning activities, the rest of the period of comparatively high temperature, confined chiefly to September (Fig. 15), is characterized by resorption of gonads and accumulation of glycogen. Resorption is brought about principally by phago-leucocytic cells which enter the follicles not through the follicular walls, as in American oysters (Loosanoff, 1942), but directly through the blood vessels (Figs. 10 and 11). Accumulation of glycogen is demonstrated by development of masses of connective tissue containing it, which rapidly fills almost the entire area between the digestive gland and the body wall of the oyster. The follicles, situated as islands within this tissue, are small, contracted and often filled with phagocytic cells (Fig. 12).

Strangely enough, simultaneously with completely spawned individuals there are still apparently normal oysters that have undischarged sex cells. These vary from those that retain only few cells in the follicles, or at least in genital canals, to those that carry virtually an undischarged supply of gametes. These individuals

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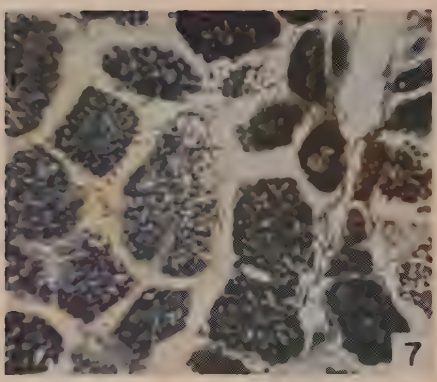
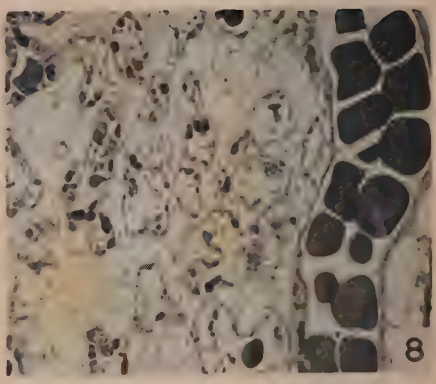
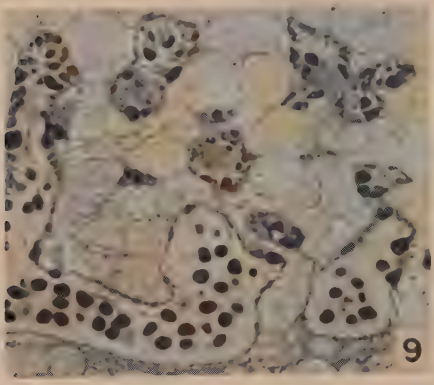
and surrounded by large areas of connective tissue. × 80.

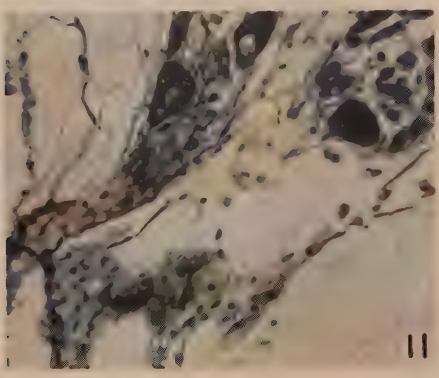
FIGURE 5. Ambisexual gonad in early stages of spring gametogenesis. × 80.

FIGURE 6. Predominantly female gonad during spring gametogenesis. Note absence of leucocytes (lymphocytes) outside of follicular wall, and connections between blood vessels and follicles. × 80.









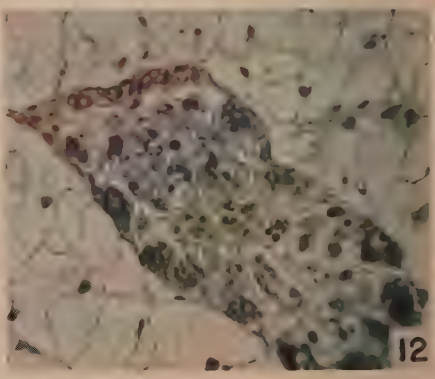


FIGURE 7. Portion of male follicles showing groups of cells in different stages of development. Sperm-balls, characterized by presence of tails of spermatozoa, are seen in the center. × 345.

FIGURE 8. Ambisexual gonad during last stages of spawning. Remnants of male cells and some undischarged eggs can be seen in shrunken follicles, while a number of ripe eggs in the process of discharge are concentrated in the genital canal. × 80.

may belong to all categories, including both strongly defined groups, *i.e.,* those predominantly males and those that are almost pure females.

A still more confusing aspect of the situation is that in some individuals with definitely male characteristics, spermatogenesis appears to be still in progress. Furthermore, in the same individuals, and sometimes even within the same microscopic field, follicles may be located side by side, some of which are completely discharged and already resorbed, others, only partly discharged, and the third group may contain male or female cells that seem to be undergoing healthy gametogenesis. Such situations can be encountered in samples collected by the end of October and, in a few instances, even later in the year.

According to Orton (1927) the proportion of females remaining unspent at the end of the summer in English waters varies from 0 to 5%. In our case, however, the proportion was significantly higher, in some samples exceeding 25%.

In discussing the fate of unspawned eggs, Orton (1927, p. 974) suggested that the oysters eventually dispose of these cells in two ways: some ova may be either retained in the gonad and become resorbed or "they may be included in egg-cysts and extruded in masses and excreted *en bloc* on to the internal face of the shell and covered over with nacreous or horny matter in the form of an excretion blister." While we agree with the first method suggested by Orton, we cannot accept his second suggestion which has not been supported by any reliable observations.

Striking differences in the condition of the gonad of the European oyster at the end of the spawning period in Boothbay Harbor probably suggest that we did not deal with a homogeneous population, but a group composed of representatives of physiologically-different races. Loosanoff and Engle (1942) and Loosanoff and Nomejko (1951) have demonstrated the existence of such physiologically-different races of the American oyster, *C. virginica,* along our Atlantic coast. These races require different minimum temperatures for development of gonads and inducement of spawning. In general, the breeding temperature requirements of the northern oyster are lower than those of the southern group. Korringa (1957) came to a similar conclusion regarding European oysters. He stated that the general population of that species is composed of several distinctly different physiological races which require different temperatures to carry on normal propagation activities.

Since French seed oysters are sometimes imported for cultivation in Holland, it is quite probable that within the sample sent to us there were individuals the genetic complex of which was such that their temperature requirements for reproduction were higher than those of the true northern oysters of Holland. As a result, because of the short, cold summers of Boothbay Harbor, these oysters were unable

FIGURE 9. Partly discharged predominantly male gonad. Groups of sperm-balls are seen in the genital canal, while many follicles are contracting and are invaded by phago-leucocytic cells. × 80.

FIGURE 10. Resorption of gonad of *O. edulis* after spawning. Note shrinking follicles and connections between follicles and blood vessels. × 80.

FIGURE 11. Migration of phago-leucocytic cells from blood vessels into apices of follicles. × 775.

FIGURE 12. Follicles in last stages of resorption. Large group of phago-leucocytic cells occupying lumen. Young sex cells along follicular walls can be seen. × 345.

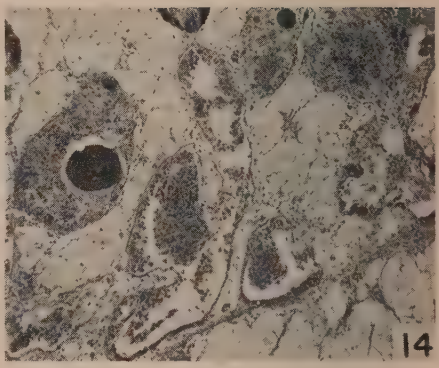


FIGURE 13. Cytolysis of predominantly female gonad that failed to ripen and be discharged. Note differences of degree of cytolysis of ovocytes in different follicles and also absence of phago-leucocytic cells outside follicular walls. × 80.

FIGURE 14. Advanced stages of resorption of predominantly female gonad. Follicles are filled with large numbers of phago-leucocytic cells. × 80.

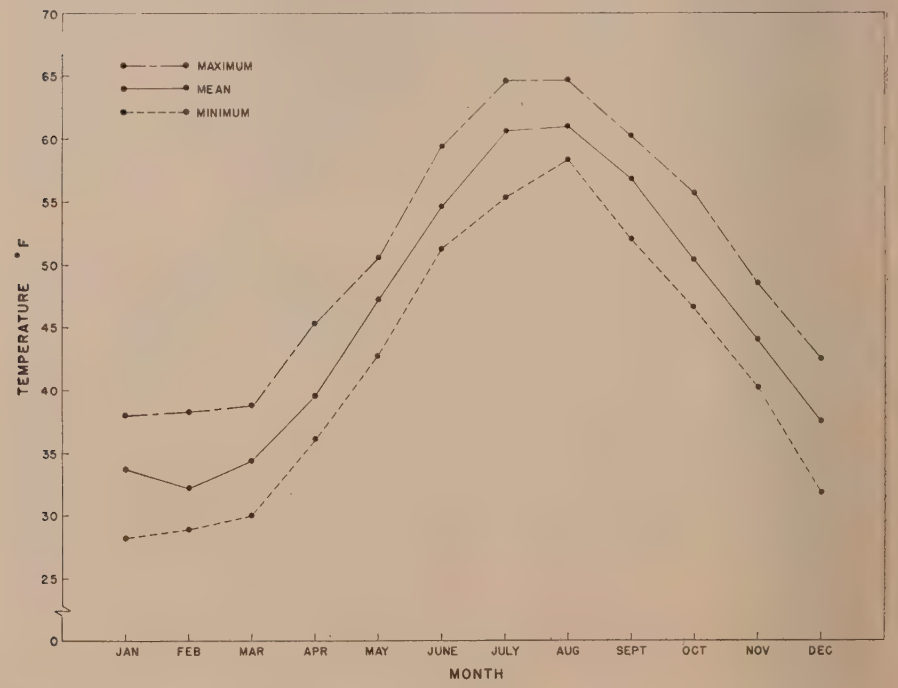


FIGURE 15. Mean, maximum and minimum monthly water temperatures at Boothbay Harbor, Maine during the period from 1906 to 1948.

to discharge their spawn. If the original shipment of European oysters, from which our samples for histological studies were collected, did include such races, it is quite probable that only the individuals carrying certain combinations of genes were able to propagate in Boothbay Harbor and are, therefore, responsible for the new population, which is now found in inshore areas of Maine (Welch, in press).

Studies of gonads collected late in November and December indicate that oysters can roughly be classified into two groups. In the first, resorption is almost or already completed. The follicles may be still full of phagocytes but, nevertheless, some young cells may be found along their walls. However, these cells are not differentiated.

The second group consists of individuals in which resorption of unspent sex cells is far from complete. Superficial examination may suggest that gonads are in the middle or at the beginning of the spawning period, but more detailed studies will show that cytolysis of undischarged cells, especially eggs, is in progress (Fig. 13). Thus, at this time of the year, as during other periods, there are pronounced individual differences between the condition of gonads of different oysters even if they belong, in general, to the same sex group.

Resorption of unspent cells continues through the winter. In some cases, it extends into April and perhaps even the first week of May, apparently depending upon individual conditions of the animals at the end of the preceding spawning season. However, at the same time and in the same oysters, in some of the follicles where resorption has already been completed, spring gametogenesis may be in progress. Consequently, two processes are going on simultaneously in the same individual—constructive gametogenesis and cytolysis. The latter is most active in female follicles where large groups of phagocytic cells attack remnants of the eggs (Fig. 14) which, in their appearance, greatly differ from each other, depending upon the stage of cytolysis.

As a rule, during early May no fully formed sperm-balls are found in the male follicles, but spermatids are occasionally seen. In female follicles normally developed ovocytes are clearly distinguishable, and in well advanced females, follicles may be seen proliferating almost to the digestive gland. In this way the annual sexual cycle of *O. edulis* is completed and begins anew.

These studies were made possible through the cooperation of Messrs. John B. Glude and Walter R. Welch, of the U. S. Bureau of Commercial Fisheries, who were kind enough to take care of the European oysters kept in Boothbay Harbor and send me preserved samples of gonads. Special thanks are due to Messrs. Richard E. Reed, former Commissioner, Sea & Shore Fisheries, Maine, and Dana E. Wallace, who were extremely helpful in overcoming a number of difficulties in connection with the introduction of *O. edulis* into this country.

Summary

1. Active spring gametogenesis begins in May.

2. General spawning begins approximately during the second or third week of July and continues until about the end of August.

3. Because of short, cold summers, usually only one sex phase is completed by an individual oyster.

4. Resorption of gonads is carried principally by phago-leucocytes which enter the follicles not through the follicular walls, as in American oysters, but directly through the blood vessels.

5. Resorption of gonads may continue throughout the winter and early spring.

6. Differences in conditions of gonads of *O. edulis* planted in Boothbay Harbor suggest that the original group was not composed of a homogeneous population, but consisted of different physiological races.

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Effects of Turbidity on Some Larval and Adult Bivalves

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Effects of Turbidity on Some Larval and Adult Bivalves

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Abstract

The article is devoted to an analysis of the experiments on effects of turbidity upon larval and adult bivalves. Studies of the American oyster, **Crassostrea virginica,** the larvae of the same species, and of **Venus mercenaria** are emphasized although several other species are also considered. Turbidity was caused by several substances, including natural silt and the clay-like substance, kaolin. Exposures of adult mollusks lasted from three hours to several weeks. Larvae of oysters and clams were grown in different concentrations of turbidity for periods as long as two weeks. Very small quantities of silt, etc., sometimes stimulated normal activities of adult and larval mollusks. This may be due to absorption by particles of suspended materials of toxic substances present in the water and to slight mechanical stimulation of the gills of adults. However, concentrations as small as 0.1 of one gram per liter of water significantly reduced the rate of water pumping and strongly affected the character of shell movements of the adults. Different turbidity-creating substances, when present in the water in the same concentrations, affected the experimental animals in a different degree. Different species of mollusks, their eggs and larvae were affected to different degrees by the same concentrations of the same turbidity-creating substances. Results suggested extension of the studies to sizes and shapes of suspended particles and to determining whether effects are mechanical or chemical. Data indicated that lamellibranchs feed most effectively in relatively clear water.

INTRODUCTION

SINCE OYSTERS, CLAMS, AND MUSSELS are widely distributed and constitute important fisheries, various aspects of their biology have been extensively studied. Baughman's (1947) bibliography of oysters, alone, contains references to thousands of articles devoted to the biology and ecology of these mollusks. Since the appearance of Baughman's review, many new articles have been

written about oysters, principally *Crassostrea virginica* and related forms, including the hard shell clam, *Venus mercenaria,* and the common edible mussel, *Mytilus edulis.*

A study of the literature shows that efforts directed toward understanding the biology of these bivalves have not been equally distributed but confined, as a rule, to selected fields which, at one time or another, appeared to be in vogue among biologists. For example, while salinity and temperature and their effects upon bivalves have been described and discussed by many authors, studies of the effects of other environmental factors, such as turbidity, have been virtually neglected. This lack of interest has persisted even though many important bivalves are inhabitants of shallow waters of estuarine regions, where turbid conditions are often created by river discharge, wind action, or dredging operations.

Obviously, it is of interest to biologists, shellfish growers, and administrators to know how turbidity affects various mollusks and their larvae. This knowledge is also needed to evaluate the numerous complaints that are brought against either the U.S. Corps of Army Engineers or dredging companies engaged in operations which result in an abnormally high turbidity of the water over shellfish beds. If dredging is carried on during the summer, when mollusks are propagating, and setting is a failure, dredgers are accused of, and often sued for, creating unfavorable conditions for the existence of bivalve larvae. During these lawsuits, and similar legal proceedings, federal and state biologists are often requested to testify or act as experts. Unfortunately, since there are few experimental data on the effects of turbidity on bivalves of different species and ages, people who act as experts have little material on which to base their opinions. This is especially true in relation to larvae, which were assumed to be extremely sensitive to abnormal turbidity. Because until recently no dependable method for growing bivalve larvae was known, obviously, no systematic studies of the effects of environmental factors upon these organisms could be conducted. Fortunately, such a method has been developed and is now widely used in many laboratories and several commercial shellfish hatcheries (Loosanoff, 1945, 1954; Loosanoff and Davis, 1950).

The purpose of this article is to review the studies on effects of turbidity on larval and adult bivalves made during recent years. Before proceeding with a discussion of the experimental results it may be advantageous to mention that the rate of water propulsion in an adult bivalve or, as we call it, the rate of water pumping, a criterion of physiological activity, has been determined by different methods and under different conditions for a number of species, especially oysters. These studies were reviewed recently, at considerable length, by Jørgensen (1955, 1960). Because of these excellent reviews it is not necessary to discuss again the various aspects of this broad field. It will be sufficient to mention, for those who are not too familiar with the anatomy of bivalves, the contributions of Kellogg (1915), Yonge (1928) and Nelson (1938), which describe the feeding and water propulsion organs of these mollusks. We may also refer to the studies on the behavior of adult oysters, *C. virginica,* exposed to different concentrations of unicellular algae, including *Chlorella* sp., *Nitzschia closterium,* and *Prorocentrum triangulatum,* which showed that these mollusks fed most efficiently when the numbers of food cells were relatively small (Loosanoff and Engle, 1947) or when the water contained little suspended material (Loosanoff and Tommers, 1948). This

point of view was in agreement with the theoretical deductions of Kellogg (1915) and Yonge (1928).

On the other hand, Lunz (1938), in his studies of the gross effects of dredging upon oysters in South Carolina waters, came to the conclusion that these operations were not injurious to oysters because he could establish no correlation between the condition of the oyster meats and the turbidity caused by dredging. Moreover, he maintained that dredging operations, regardless of the considerable turbidity that they created, did not unfavorably affect the spawning of oysters or setting of their larvae. In other words, according to Lunz, oysters in the areas where the dredging was carried on, remained practically undisturbed, even though the water was made quite turbid.

Considering the discrepancy between Lunz' conclusions and ours, it was thought desirable to verify at least some aspects of the question in dispute by designing and executing a series of critical experiments which could show convincingly the extent of the effects of turbidity-creating substances upon the behavior of some bivalves.

METHODS

The oysters used in the experiments were selected for their uniformity. They were about four years old and measured between 90 and 95 mm in length and 60 to 68 mm in width. Their average volume was approximately 95 cc. Before being used the oysters underwent a period of observation to ascertain that no sick individuals were in the group. Furthermore, to be certain that the oysters were not unduly disturbed or handled too much immediately prior to being used in the experiments, the rubber aprons employed in determining their rate of water pumping were attached to their shells several weeks prior to the beginning of the observations.

The methods employed in these studies were virtually the same as those in our observations on effects of different concentrations of microorganisms upon feeding activities of adult oysters (Loosanoff and Engle, 1947). During these experiments shell movements and rate of water pumping by oysters, under normal conditions and after the addition of different quantities of turbidity-creating substances, were recorded on kymographs. Considering the importance of observing undisturbed mollusks, so strongly advocated by MacGinitie (1941), the oysters were placed in the running water of the apparatus chamber at least 12 hours before an experiment was begun. At that time the only change was the starting of the kymograph, which in no way reflected on or was felt by the oysters because the kymograph was located on a stand not connected with the oyster chamber foundation and, furthermore, was supported by a thick rubber mat to eliminate disturbing vibrations.

After the oysters had been in flowing sea water for several hours and their normal pattern of behavior had been recorded, turbid water was introduced into the chamber. This, again, was accomplished merely by manipulating a series of cocks without disturbing the oysters. After the experimental animals had been in the turbid water for the required time, regular sea water was substituted for the turbid water, again by merely opening and turning off cocks.

During the studies the temperature of the water ranged between 17.0° and 23.0°C, the salinity was steady near 27.0 parts per thousand and the pH of silt suspensions and of sea water ranged from 7.9 to 8.1. Provisions were made so that the temperatures of the turbid and regular sea water did not vary from each other by more than 0.5°C. Since presence of silt in water can considerably reduce the quantity of dissolved oxygen, the turbid water was

always vigorously aerated. This method was also helpful to drive out unwanted gases that may form in the water because of the addition of silt and other substances.

The materials used to make sea water turbid were fine silt collected from the tidal flats of Milford Harbor; kaolin (aluminum silicate), a clay-like substance; powdered chalk; calcium carbonate; and Fuller's earth (Loosanof and Tommers, 1948). The latter, however, was used in only a few experiments. All these materials are sometimes found under natural conditions in estuarine waters. Silt, a complex mixture of inorganic and organic materials, is very common, of course, and is usually present in various quantities in sea water. Heavy rains resulting in a heavy river discharge, dredging, and also boat traffic may noticeably increase quantities of suspended silt. Kaolin, as well as other clay-like substances, is often found in various mixtures of soils that form foundations of oyster beds. Large quantities of clay are also brought down by rivers. Since oyster shells are made largely of calcium carbonate, minute particles of this substance can often be found suspended in the water over oyster beds. Fuller's earth, which consists chiefly of shells of small diatoms, is also a natural material.

The silt used in the experiments was prepared as follows: Soft mud collected from the upper layer of the tidal flats of Milford Harbor was agitated in river water. The heaviest particles were permitted to settle and then discarded, while the material still in suspension was filtered through a No. 20 plankton net. This fine suspension was kept in glass vessels until it settled to the bottom, a procedure which sometimes requires several days. The water was then decanted and the silt dried in the sun in large enamel trays. The dry material was later pulverized and placed into air-tight jars. Before using the material it was resuspended in the water, in the form of minute particles, by prolonged, vigorous stirring.

RESULTS

Silt was the first material to be studied. Even when such a small quantity of silt as 0.1 g/liter was present, the behavior of the adult oysters was noticeably affected (Figure 1). For the group as a whole, the average reduction in the

FIGURE 1. Kymograph record of shell movements (1st line) and rate of pumping (2nd line) of an oyster kept for the first three hours in normal sea water and then exposed to turbid water containing 0.1 g/liter of silt. Each vertical mark of the second line designates the discharge of 278 cc of water pumped by the oyster.

rate of pumping was 57 per cent and in more severe cases the decrease was nearly 90 per cent (Table 1). In one or two instances, however, the oysters appeared to be stimulated and pumped faster. Even at this low concentration of silt the type of shell movement was changed indicating that the oysters were not acting normally.

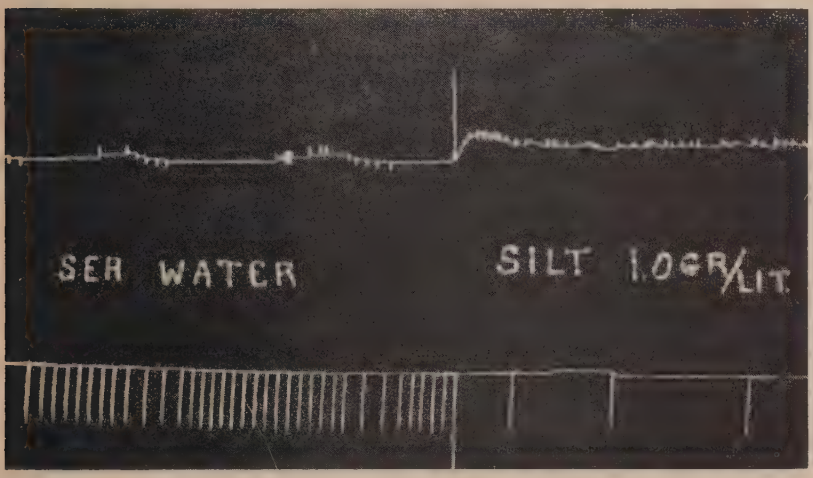

FIGURE 2. Kymograph record showing shell movements (1st line) and rate of pumping (2nd line) of an oyster subjected to sea water and then to turbid water containing 1.0 g/liter of silt. Each vertical mark on the second line designates the discharge of 237 cc of water pumped by the oyster.

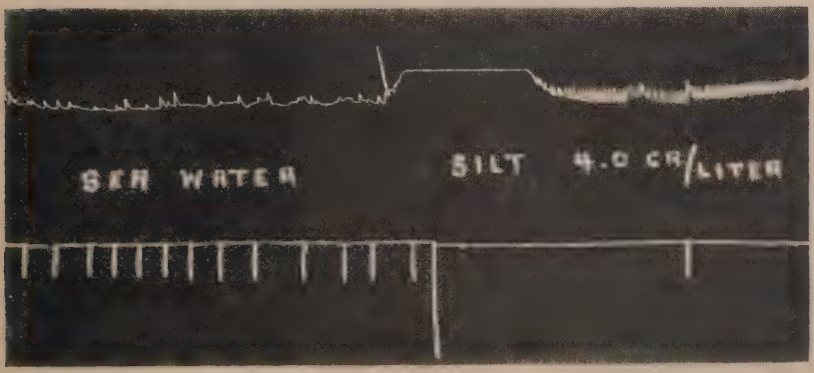

FIGURE 3. Kymograph record of shell movements (1st line) and rate of pumping (2nd line) of an oyster exposed to normal sea water and then to turbid water containing 4.0 g/liter of silt. Each vertical mark of the second line designates the discharge of 272 cc of water pumped by the oyster.

TABLE 1

EFFECTS OF DIFFERENT CONCENTRATIONS OF TURBIDITY-CREATING SUBSTANCES ON PUMPING RATES OF OYSTERS. RATE OF PUMPING IN SEA WATER AT THE BEGINNING OF THE EXPERIMENTS WAS TAKEN AS 100 PER CENT.

Substance	Concentration g/liter	Number of Oysters	Range of Change in %	Average Reduction in %
Silt	0.1	22	+18 to — 87	57.0
"	0.25	21	—12 to — 92	74.5
"	0.5	16	+15 to —100	68.5
"	1.0	22	—18 to —100	81.0
"	2.0	17	—41 to —100	85.0
"	3.0	10	—83 to —100	93.7
"	4.0	18	—62 to —100	94.0
Kaolin	0.1	24	+16 to — 77	46.0
"	0.25	22	—35 to — 95	68.0
"	0.5	25	+10 to — 93	68.5
"	1.0	16	—14 to —100	71.0
"	2.0	15	—66 to —100	78.0
"	4.0	16	—27 to — 95	85.0
Chalk	0.1	18	—12 to — 59	38.0
"	0.5	18	—44 to — 86	76.0
"	2.0	18	—68 to — 94	87.0
"	4.0	19	—79 to — 94	89.0
Fuller's Earth	0.5	8	—32 to — 80	60.0

Greater concentrations of silt resulted in stronger effects on both shell movements and rate of water pumping (Table 1, Figure 2). In such heavy concentrations as 3.0 and 4.0 g/liter the average reduction in rate of pumping was over 90 per cent (Figure 3).

Although such large quantities of silt seldom occur in nature they may, nevertheless, be created during a period of unusually heavy floods or occur, and sometimes persist for weeks or months, within areas where extensive dredging is carried on, especially if the methods employed are such that large quantities of disturbed bottom material are allowed to escape into the water.

In turbid waters the oysters formed and discharged large quantities of silt-containing pseudo feces. Stomach examinations, however, showed that not all of the silt was rejected in this way; some was ingested, together with large quantities of mucus that was formed by the gills. In some instances, although the shells remained open and moving, the oysters did not pump. Occasionally, especially in heavier concentrations of silt, the oysters closed their shells entirely for extended periods. In long-term experiments not discussed in this paper oysters sometimes remained closed for a period of several weeks, opening their shells slightly from time to time, as if testing the water, and then closing the shells again without resuming pumping.

The shell movements of oysters kept in turbid waters were clearly associated with frequent ejection of large quantities of silt and mucus accumulating on the gills and palps. These movements closely resembled those of oysters which were kept in heavy concentrations of live microorganisms, such as *Chlorella, Nitzschia,* or commercial yeast (Loosanoff and Engle, 1947). Thus, the results of these two series of studies showed a strong similarity in the behavior of oysters in turbid waters regardless of whether the turbidity was caused by a large number of live microorganisms or merely common silt.

This similarity was even more strongly emphasized by observations that in both series of experiments, when the flow of silt or plankton-laden water was substituted with regular sea water, the oysters quickly recovered and both the rate of pumping and shell movements returned to normal (Figure 4). The behavior of oysters during the recovery period resembled the so-called "cleansing reaction" which we noted in the above-mentioned studies on feeding of oysters when large quantities of phytoplankton cells were present in the water. The consistency of our results, therefore, strongly supports the contention that lamellibranchs, such as oysters and clams, feed most efficiently in relatively clear water. This contention remains valid even though Yonge (1948) showed that some bivalves, such as *Spisula subtruncata,* are provided with special anatomical adaptations to live in silty environment. These forms, therefore, may not be regarded as strictly clear water inhabitants but, nevertheless, it has not been disproven experimentally that they, too, feed more effectively in clearer waters.

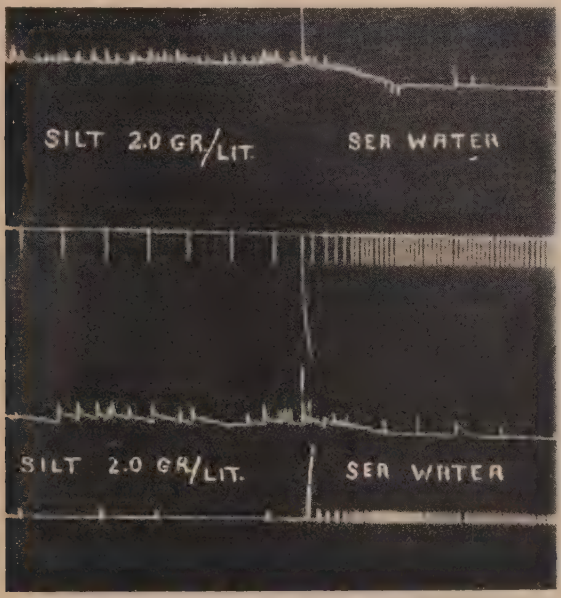

FIGURE 4. Kymograph record showing shell movements (1st & 3rd lines) and rates of pumping (2nd & 4th lines) of two oysters exposed to turbid water containing 2.0 g/liter of silt and then to normal sea water. Each vertical mark on the 2nd line designates the discharge of 244 cc of water pumped by one oyster, while each mark on the 4th line shows the discharge of 251 cc of water pumped by the second oyster.

Another series of experiments was designed to determine whether a gradual, rather than a sudden increase in turbidity is better tolerated by oysters. As usual, the oysters were kept in running sea water until they opened their shells and began pumping. After the normal pattern of each oyster's

FIGURE 5. Kymograph record showing shell movements (1st line) and rate of pumping (2nd line) of an oyster exposed to gradually increasing concentrations of silt ranging from 0.1 g/liter to 0.5 g/liter. The oyster remained in each concentration for 2 hours. Each vertical mark on the second line designates the discharge of 250 cc of water pumped by the oyster.

behavior was established they were exposed to a concentration of 0.1 g/liter of sea water. Again, regardless of the low silt concentration, the oysters showed, by the change in their shell movements and reduction in rate of pumping, that they were unfavorably affected (Figure 5). After two hours the concentration of silt was increased to 0.25 g/liter and, after an equal period of time, to 0.5 gram. Under these conditions the rate of pumping decreased progressively with each increase in the concentration of silt and some oysters showed a typical "fighting" type of shell movement, indicating that they were expelling feces. After exposure to a concentration of 0.5 gram of silt the sea water was turned on to replace the turbid water. Within a few minutes all oysters resumed active pumping at a significantly faster rate.

In such stronger concentrations of silt as 1.0, 2.0, 3.0, and 4.0 g/liter, in each of which the oysters remained for two hours, they were strongly affected but, nevertheless, even in the heaviest concentration a few oysters continued to pump some water. However, a comparison of the rates of pumping recorded during the initial experiments with those in which the turbidity was increased gradually failed to show that because of the gradual increase in turbidity the rate of pumping was more normal.

Another experimental approach consisted of observing oysters when they were exposed to silt for relatively long periods, extending for 48 hours. The concentrations used were 1.0, 2.0, 3.0, and 4.0 g/liter. Regardless of heavy concentrations, the oysters, if taken as a group, remained open more than half the time, although some of them were open only 8 per cent of the total time. However, even among the oysters that remained open some did not pump water at all and, in general, the pumping rate was reduced approximately 90 per cent. The shell movements were abnormal, clearly different from those exhibited by the same oysters while still in regular sea water.

When, after the 48-hour exposure to turbid water, the oysters were again subjected to the flow of normal sea water, many of them, for some time, did not show the usual recovery-type of shell movement nor did they resume a rapid rate of pumping, as is normally observed after exposure of oysters to turbid water for relatively short periods. Apparently, longer exposures affected them unfavorably, perhaps by injuring the delicate ciliary mechanisms of their gills and palps. This conclusion is strongly supported by our other long-range experiments, not discussed in this article, where oysters and sea mussels, *M. edulis,* eventually died if kept in turbid water for several weeks.

Mortality will occur only if mollusks are kept in relatively large quantities of water, not less than 25 or 50 gallons per individual. Under radically different conditions, such as those employed by Fox, Sverthrup and Cunningham (1937),

where a large mussel was placed in a small quantity of water, sometimes only 1.0 liter, the mollusk will be able, within a few minutes, to remove from suspension the turbidity-producing substances, rendering the water clear. When placed in a large quantity of water, however, the mussel or oyster may pump vigorously at first, removing from the water, in the form of pseudo feces, some algae or silt, but will become exhausted long before the turbidity is significantly lowered, cease pumping and close its shell. Eventually, the animal dies.

Mortality of experimental mollusks kept for long periods in large quantities of water containing heavy concentrations of turbidity-creating substances was probably due, in part, to clogging of the gills with silt or other materials, which interfered with normal respiration and feeding of these bivalves. The relatively high temperature at which these experiments were conducted (about 20°C) also probably contributed to the lethal effect. Being unable to open their shells and cleanse their gills, these animals were, nevertheless, compelled to function at a rapid metabolic rate and, as a result, soon died from starvation and suffocation. This inference appears logical because at the above temperature *M. edulis* in our waters normally feeds from 97 to 99 per cent of the time (Loosanoff, 1942), while *V. mercenaria* and *C. virginica* remain open, and probably feeding, approximately 90 per cent of the time (Loosanoff, 1939; Loosanoff and Nomejko, 1946). Ellis (1936) also showed that erosion silt strongly interfered with the feeding of fresh water mussels because they remained closed between 75 to 95 per cent of the time. In Ellis' experiments, mussels that died in turbid water always contained large quantities of silt in the mantle cavity and gills, a condition that we also observed in dead and dying *C. virginica* and *M. edulis* used in our long-term experiments.

Studies of oxygen consumption in various species of oysters, mentioned by Jørgensen (1960), show that it is tripled when the water temperature rises from 10° to 28°C and doubled when it rises from 16° to 28°C. Jørgensen concludes, therefore, that within their natural range of existence feeding conditions for bivalves became poorer at higher temperatures. Since our experiments were conducted at relatively high temperatures and since, because of turbidity, the oysters could not feed effectively, their uncompensated rapid metabolic rate was an indirect cause of the comparatively rapid death.

In concluding the description of the effects of silt upon oysters it should be mentioned that the addition of minute quantities, considerably smaller than 0.1 g/liter, may often reflect favorably on the behavior of oysters by inducing somewhat more rapid pumping. This observation is identical to that made in our studies of feeding oysters with different quantities of living algae (Loosanoff and Engle, 1947). We agree with Jørgensen (1955) that when only very small amounts of suspended matter are present in the water the rate of pumping may be independent of these concentrations.

Clay-like kaolin was the second material used to make the water turbid. Concentrations ranged from 0.1 to 4.0 g/liter. As in the case of common silt, even such small quantities of kaolin as 0.1 g/liter considerably decreased the rate of pumping of oysters and also somewhat changed the character of their shell movements (Table 1, Figure 6). As the concentration increased, the abnormal aspects of the behavior of oysters became gradually more prominent (Figure 7). When concentrations were as high as 3.0 or 4.0 g/liter (Figure 8) the shell movements became abnormally vigorous, indicating that the oysters were continuously cleansing their gills. As usual, large quantities of pseudo feces were discharged under these conditions but, nevertheless, some oysters kept

their shells open for long periods and pumped water, although the rate of pumping was markedly reduced.

As in the experiments with silt, the oysters, when again exposed to regular sea water, quickly resumed a normal or even faster-than-normal rate of water pumping and their shell movements also soon became normal.

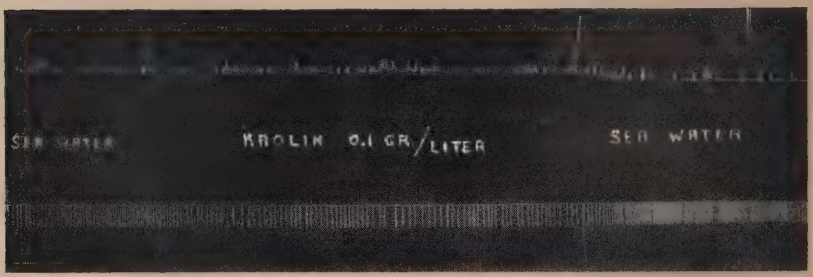

FIGURE 6. Kymograph record showing shell movements (1st line) and rate of pumping (2nd line) of an oyster exposed to sea water, then to a concentration of 0.1 g/liter of kaolin, and returned to sea water. Each vertical mark on the second line designates the discharge of 255 cc of water pumped by the oyster.

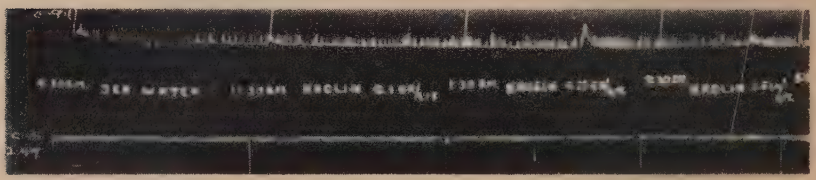

FIGURE 7. Kymograph record showing shell movements (1st line) and rate of pumping (2nd line) of an oyster exposed to sea water and then to gradually increasing concentrations of kaolin ranging from 0.1 g/liter to 0.5 g/liter. Each vertical mark on the second line designates the discharge of 245 cc of water pumped by the oyster.

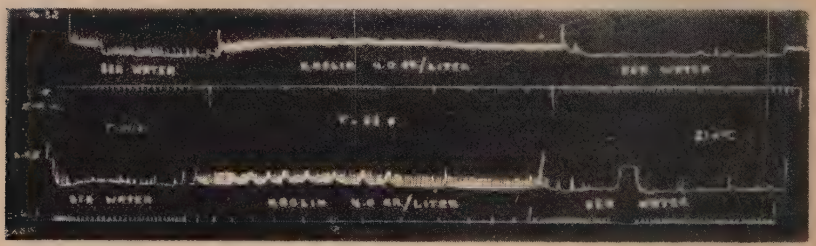

FIGURE 8. Kymograph record showing shell movements (1st & 3rd lines) and rates of pumping (2nd & 4th lines) of two oysters exposed to sea water, then to a concentration of 4.0 g/liter of kaolin, and again to sea water. Each vertical mark on the second line designates the discharge of 249 cc of water and the fourth line, 265 cc of water pumped by the oysters.

Experiments with pulverized chalk (calcium carbonate) closely corroborated the conclusions formed during studies of effects of two other turbidity-creating materials (Table 1). Again, the presence of chalk in the water depressed the rate of water pumping and usually radically changed the type of shell movement (Figure 9). After the oysters were returned to sea water they quickly showed signs of recovery.

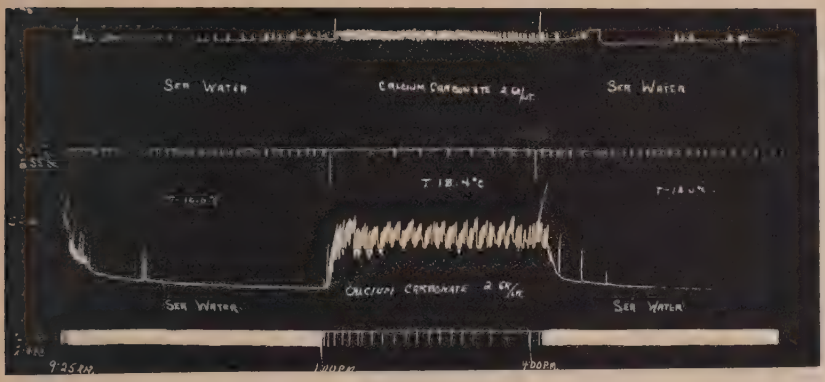

FIGURE 9. Kymograph record showing shell movements (1st & 3rd lines) and rates of pumping (2nd & 4th lines) of two oysters exposed to sea water, then to a concentration of 2.0 g/liter of chalk and again to sea water. Each vertical mark on the second line designates the discharge of 255 cc of water and the fourth line, 219 cc of water pumped by the oysters.

A limited number of experiments in which Fuller's earth was used supported, in general, the conclusions formed during observations on the action of the three other materials.

Observing the development and survival of molluscan eggs, especially during early stages in different concentrations of silt and related substances is, of course, a necessary and important step in evaluating the effects of turbidity. However, as already mentioned, until recently no reliable studies could be made of various aspects of larval physiology or ecology because no simple, standard method for cultivation of bivalve larvae was available. Since the new method was developed, it has been used extensively in studying various ecological requirements of larvae, including their reactions to turbidity. This work has been carried on at our laboratory by Harry C. Davis.

Davis, using the same turbidity-creating substances that were employed in earlier experiments with adult oysters (Loosanoff and Tommers, 1948), studied their effects on eggs and larvae of oysters, *C. virginica,* and clams, *V. mercenaria.* The methods employed in these studies, including use of a rotating wheel to maintain turbidity at definite constant levels, have already been described (Davis, 1960).

Davis found that silt was much more harmful to oyster eggs than to those of clams (Table 2). For example, in concentrations of only 0.25 g/liter of silt only about 73 per cent of the oyster eggs survived, while over 95 per cent of the clam eggs developed to straight hinge stage. In a concentration of

0.5 g/liter practically all the clam eggs developed to straight hinge stage, while only 31 per cent of the oyster eggs survived this treatment. In stronger concentrations, 1.0 and 2.0 g/liter, practically no oyster eggs developed, while 39 per cent of the clam eggs developed normally, even at the concentration of 2.0 g/liter.

In suspensions of kaolin and Fuller's earth, on the contrary, oyster eggs showed a much higher survival than clam eggs. For example, in a concentration of 1.0 g/ liter of kaolin and Fuller's earth practically all oyster eggs developed to straight hinge stage, while only 37 per cent and 57 per cent of clam eggs survived (Table 2).

TABLE 2

PERCENTAGE OF EGGS OF OYSTERS *(C. virginica)* AND CLAMS *(V. mercenaria)* DEVELOPING TO STRAIGHT HINGE LARVAE IN DIFFERENT CONCENTRATIONS OF TURBIDITY-CREATING SUBSTANCES. THE NUMBER OF EGGS IN CONTROLS DEVELOPING TO THE STRAIGHT HINGE STAGE IS TAKEN AS 100 PER CENT (AFTER H. C. DAVIS).

Concentrations	Silt		Kaolin		Fuller's earth	
G/liter	Oyster	Clam	Oyster	Clam	Oyster	Clam
0.125	95	95	99	82	104	75
0.250	73	96	100	82	103	61
0.500	31	99	104	52	102	41
1.000	3	79	107	37	98	57
2.000	0	39	94	49	79	50
3.000	0	0				
4.000	0	0	76	42	26	45

Of the materials tried, silt was more harmful to oyster eggs than either kaolin or Fuller's earth (Table 2). In the two latter materials some oyster eggs developed normally even in concentrations of 4.0 g/liter, while in a concentration of only 1.0 g/liter of silt practically none of the eggs reached straight hinge stage.

Davis (personal communication) also found that, as in the case of eggs of the two species, silt was more harmful to oyster larvae than to clam larvae. For example, at 0.75 g/liter of silt growth of oyster larvae was significantly affected, and at 1.5 g/liter or higher concentrations, growth was negligible. No oyster larvae survived in concentrations of 3.0 and 4.0 g/liter. As a striking contrast, clam larvae grew normally in a concentration of 1.0 g/liter of silt. The majority survived for 12 days and even showed some growth in 3.0 and 4.0 g/liter. However, it is doubtful that any clam larvae could grow to metamorphosis at these two concentrations.

Again, as with eggs of the two species, kaolin and Fuller's earth were less harmful to oyster larvae than to clam larvae. Whereas 0.5 g/liter of kaolin caused approximately 50 per cent mortality of clam larvae in 12 days, and virtually no clam larvae survived in concentrations of 1.0 g/liter of either Fuller's earth or kaolin, growth of oyster larvae was not appreciably affected by 1.0 g/liter of kaolin.

Davis also established the remarkable fact that some oyster larvae may survive for at least 14 days in concentrations of 2.0 g/liter of silt and up to 4.0 g/liter of kaolin or Fuller's earth.

When minute quantities of silt, kaolin or Fuller's earth were added to water containing straight hinge larvae of these species, growth of these organisms was stimulated, often exceeding that of controls. It is thought that this was a result of adsorption by particles of suspended material of the toxic substances produced in larval cultures by bacteria or algae. It is also possible that some of the particulate materials added to the water of larval cultures carried along a positive growth factor as some soil solutions do. In view of the consistency of such results these possibilities should be investigated so that, perhaps, methods based on these findings can be developed to improve handling of larval cultures of different aquatic invertebrates.

DISCUSSION

This article is devoted principally to an analysis of the studies of effects of turbidity on adult oysters, a brief account of which has already been presented (Loosanoff and Tommers, 1948), and of recent studies by my associate, H. C. Davis, on effects of turbidity on larvae of our two most common bivalves, the American oyster, *C. virginica,* and the hard clam, *V. mercenaria.* These studies, together with Ellis' (1936) work on fresh water mussels, Fox et al (1937) on the California mussel, *Mytilus californianus,* and Jørgensen (1949, 1955, 1960), are the few experimental contributions available at present.

The majority of the observations on adult oysters were of comparatively short duration, the oysters being kept in turbid water from 3 to 6 hours. However, even these observations strongly pointed to the conclusion that oysters are very sensitive to turbidity, regardless of what particulate materials are responsible for it.

When the turbidity of the water is noticeably increased, the oysters begin to react to it by decreasing their rate of water pumping and by changing the character of shell movements which, in stronger concentrations of turbidity-creating substances, clearly indicates that the oysters are seriously disturbed physiologically. In general, there is a correlation between increase in turbidity and decrease in rate of pumping (Table 1). In strong concentrations oysters may cease pumping entirely. Eggs (Table 2) and larvae of bivalves are also affected by heavy turbidity, although they seem to display considerable tolerance toward certain substances. Larvae of different species may react differently.

When adult mollusks were exposed to different concentrations of silt-laden water for periods lasting 48 hours, they were affected at the end of this period and their recovery, upon return to normal sea water, was considerably slower than after shorter exposures of only a few hours. It is assumed that the delicate ciliary mechanism of the gills and palps of the experimental bivalves was somewhat injured during the longer exposures.

If subjected to even more prolonged exposures in turbid water, mollusks eventually die because under such conditions they are not able to respire or feed normally. If, instead of a sudden exposure of the oysters to turbid water, they are submitted to slow and gradual increases in turbidity, the shell movements and rate of water pumping are not basically different from those observed in the same concentrations when the oysters experience a relatively rapid transition from clear to turbid water.

Oysters, and some other bivalves from different geographical regions, may display different physiological capabilities by showing different levels of tolerance to the same degrees of turbidity. Our observations were made on

Long Island Sound oysters, which are accustomed to living in comparatively clear water. In other sections of our Atlantic coast, North and South Carolina for example, oysters exist in waters which are extremely turbid. Perhaps these southern oysters, which seem to show a greater tolerance to turbidity, belong to groups that are physiologically different from the northern, clear water oysters. Studies comparing the behavior of oysters of these different geographical groups under the same turbidity conditions would be extremely desirable and informative.

According to Jørgensen (1955) different species of bivalves are not equally sensitive to the same amounts of turbidity in sea water. Jørgensen also appears to share our contention that different groups of the same species may show a difference in tolerance towards the presence of suspended silt, depending upon the condition of their normal habitat; in other words, they may display differences which we believe may exist between the northern and southern oysters *(C. virginica)*. Recent studies of Imai and Sakai (1961) on the Japanese oyster, *Crassostrea gigas,* also show that local races display differences in adaptability to environmental conditions.

It is also possible that even though southern oysters do live in turbid waters, their existence, to a certain degree, is unfavorably affected by this condition. This is a possibility because in spite of the long periods of warm weather, during which southern oysters are able to feed, their meats are normally much poorer than those of oysters of the New England or Middle Atlantic states where summers are much shorter. This is clearly demonstrated by the ratio of pounds of meat shucked per standard bushel of oysters grown in the different areas. Perhaps turbidity is not the only factor contributing to the relatively poor condition of the meats of southern oysters. Diseases and long spawning periods may be partially responsible also but, nevertheless, turbidity cannot be entirely dismissed as one of the factors involved.

Several aspects of the studies mentioned in this article should be considerably expanded. For example, effects on the same organism of different particulate materials present in the same concentrations should be determined and understood. This will extend the observations to sizes and shapes of suspended particles and to their effects on eggs, larvae and, finally, adult animals.

We know that certain lamellibranchs possess the ability to select, by the elaborate sorting devices of the gills, food particles from suspended matter (Loosanoff, 1949; Jørgensen, 1955), while other species do not possess this ability. Studies of this nature, extended to a number of filter-feeding forms, will show whether the effects of different particulate substances are purely mechanical, purely chemical or a combination of the two.

This will also lead to an understanding of the biological significance of the conglomerates of the particulate material in sea water which, at times, exist in large quantities in such places as Long Island Sound. According to Dr. Gordon Riley of Yale University (personal communication) the base of the aggregates is an amorphous material of uncertain composition, consisting probably of bacterial slime with particles of silt, phytoplankton, and bacteria imbedded in it. We usually notice it in April and June, when large areas of Long Island Sound contain masses of these slimy conglomerates. However, being of unstable nature, they are easily disrupted by wave action and part of the material of which they are composed descends to the bottom where beds of clams, oysters, and other filter-feeding invertebrates are located. Obviously, the role of these aggregates, which are partly responsible for

turbidity over molluscan beds, should be determined. Still another aspect of this phenomenon, that is entirely unknown at present, is the role which the mechanical and chemical characteristics of the aggregates plays in the existence and survival of bivalve larvae. Possibly, because diatoms are found imbedded in the aggregates, bivalve larvae and eggs become trapped in them also.

It is realized that our results and conclusions expressed in this article cannot be generalized for the entire group of lamellibranchs. Our experiments should be merely considered as a pioneering step towards the solution of an important ecological problem in the existence of filter-feeding invertebrates. However, even the limited information so far obtained on this subject strongly indicates that we should always consider with caution and suspicion any conditions where turbidity of sea water in shellfish-producing regions is raised considerably above the normal level.

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V. L. LOOSANOFF, U. S. Bureau of Commercial Fisheries Biological Laboratory, Milford, Connecticut. Controlling experimental conditions in studies of eggs and larvae of aquatic forms. (30 min.)

The paper discusses the progress that has been achieved during the last decade in methods of studying eggs and larvae and, in some cases, juveniles of marine forms under conditions where various factors of the environment, singly or in groups, can be controlled with precision.

Using the new methods many invertebrates can be conditioned to spawn out of season. Oysters, *Crassostrea virginica,* and clams, *Mercenaria mercenaria,* can now be induced to spawn any day of the year. Several species of gastropods, echinoderms, worms and crustaceans can also be compelled to develop ripe eggs even in the middle of winter. Reliable production of certain species of algae in unialgal and bacteria-free cultures assures a good supply of live foods for molluscan larvae, as well as larvae of other phyla. Recently, dried algae, including such unicellular ones as *Scenedesmus* sp. and, especially, freeze-dried naked flagellates, such as *Isochrysis galbana* and *Monochrysis lutheri,* proved to be excellent foods for larvae. Antibiotics and certain chemicals help to control pathogenic bacteria in larval cultures, thus preventing mortalities due to diseases. Because of good control of environmental conditions extensive studies can now be conducted on the effect of such factors as light, temperature, salinity, turbidity, pH, quality and quantity of food, inter- and intra-specific competition and water currents on the development of young mollusks. Controlled conditions also lead to a study of the diseases of larval and juvenile mollusks and other forms, as well as open the field of selective breeding of species that are of commercial importance.

RESEARCH ACTIVITIES

By
V. L. Loosanoff, Laboratory Director
Marine Biological Laboratory
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Milford, Connecticut

Milford Biological Laboratory, located on Long Island Sound, is engaged principally in studies of ecology and physiology of marine invertebrates, especially mollusks. Most of the work is of basic nature, but the staff is also interested in certain aspects of applied zoology.

One of the oldest problems in the laboratory schedule is the study of ecological factors governing propagation of oysters and star-fish in Long Island Sound. These studies include observations on gonad development and time and intensity of spawning and setting of the above two species in relation to chemical, physical and biological conditions. Physiological studies of adult oysters also occupy an important place in our work.

Another project of considerable magnitude is the cultivation of larval mollusks to study their ecological and physiological requirements. Considerable attention is given to studies of methods of control of diseases and competitors of larvae and juvenile mollusks. These studies include isolation of marine bacteria, fungi and viruses and testing them for pathogenicity to bivalves.

Considerable progress has been made in the technique of mass culture of marine algae. Some of these, such as Isochrysis galbana, Monochrysis lutheri and Dunaliella euchlora, are widely used in experimental work.

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